CHAPTER 2-6
STREAMS: PHYSIOLOGICAL ADAPTATIONS – WATER, LIGHT, AND TEMPERATURE

TABLE OF CONTENTS

Moisture Relations 2-6-3
Drying Effects 2-6-4
Membrane Leakage 2-6-9
Rate of Drying 2-6-11
Recovery 2-6-12
Photoinhibition 2-6-12
Sucrose Accumulation 2-6-12
More Leakage Problems 2-6-13
Invaders in the Mix 2-6-13
Polyribosomes and Protein Synthesis 2-6-13
Non-autotrophic CO_2 Fixation 2-6-14
Temperature Effects 2-6-14
Pigment Responses 2-6-15
Fatty Acid Responses 2-6-15
ABA Mediation 2-6-16
Allocation Changes 2-6-17
Light 2-6-17
Habitat Differences 2-6-20
Chlorophyll and Accessory Pigments 2-6-21
Seasons 2-6-22
UV-B 2-6-22
Sun and Shade Plants 2-6-24
Photoprotective Pigments 2-6-24
Cell Wall vs Soluble Compounds 2-6-26
UV Interactions 2-6-26
Photoinhibition 2-6-27
Effects of Nutritional Status 2-6-27
Temperature 2-6-27
High Temperatures 2-6-27
Low Temperatures 2-6-29
Optimum Temperatures 2-6-30
Bryophyte Antifreeze 2-6-31
Temperature Effects on Absorption 2-6-31
Summary 2-6-31
Acknowledgments 2-6-32
Literature Cited 2-6-32

CHAPTER 2-6
STREAMS: PHYSIOLOGICAL ADAPTATIONS – WATER, LIGHT, AND TEMPERATURE

Figure 1. ***Fontinalis squamosa*** on rock above water near Swallow Falls, Wales, demonstrating that the emerged moss is still wet, thus drying slowly. Photo by Janice Glime.

In 1996, I (Glime 1996) revelled in the realization that a number of scientists were applying aquatic bryophytes in the solution of environmental problems. These included monitoring, cleanup, culturing for restoration, and even prospecting. But to take full advantage of these possibilities, we need to understand the physiology of these bryophytes that constrains their habitats and permits them to do what they do.

Loss of bryophytes due to draining waterways also impacts the fauna of the waterway. McCarthy (1977) noted that the flora and fauna of the Trimblestown River in Ireland were seriously affected by drainage. They found that the submerged ***Fontinalis*** (Figure 1) and flowering plant *Rorippa* (Figure 2) had been replaced by emergent vegetation, filamentous algae, and *Chara* (Figure 3), changing the habitats available to the fauna. Although the numbers and biomass recovered rapidly one year after the drainage disturbance, the bryophyte beds did not. Thus, for many reasons we need to understand the biology and ecology of the bryophytes that occupy streams.

Figure 2. *Rorippa* sp., member of a genus that was replaced by emergent vegetation following drainage of the waterway. Photo by Gerrit Davidse, through Creative Commons.

Figure 3. *Chara* sp., member of a genus that replaced ***Fontinalis*** following drainage of the waterway. Photo from Carolina Biological Supply Company, with online permission.

Moisture Relations

The effects of flooding disturbance in streams and rivers has been relatively well studied (Lake 2000). The effects of drought have not. Both of these conditions destroy habitat and create new habitat, creating patchiness. Biota may survive by finding refugia in some of these patches.

The presence of nearly constant water as a medium will necessarily present physiological problems for aquatic bryophytes. Although the bryophytes were derived from algae, which originated in water, the bryophytes have since that time become highly adapted to survive severe desiccation for prolonged periods of time. The freshwater bryophytes appear to have returned to the water environment from largely terrestrial lineages. Nevertheless, that history of aquatic habitats could provide conserved genes that help to preadapt these bryophytes to water. On the other hand, streams in particular can present some real challenges.

A major water problem for aquatic bryophytes arises because of seasonal and short-term changes in water level. In the summer, bryophytes can be stranded out of water for weeks at a time. When water does come, it is likely to bring abrasion and siltation. Thus, the stream bryophytes must be prepared for desiccation as well as submersion. For a long time, aquatic bryophytes were considered to be intolerant of desiccation, but later experiments proved this assumption to be wrong (Carvalho *et al*. 2011).

One can observe aquatic bryophytes such as ***Fontinalis*** species in dry stream beds in late summer (Figure 4). Glime (1971) tested this drying effect on two species of ***Fontinalis*** [***F. dalecarlica*** (Figure 5), ***F. novae-angliae*** (Figure 6)] by removing their rocks with mosses intact to the stream bank where they were not submersed for one year. Many of these mosses survived this isolation, developing new growth from stem tissue, despite the apparent death of the leaves that had been exposed to the treatment.

Figure 4. ***Fontinalis antipyretica*** in dry stream in Michigan's Upper Peninsula, USA. Photo by Janice Glime.

Figure 5. ***Fontinalis dalecarlica***, a species that can survive for one year above water if the desiccation is slow. Photo by Jean Faubert, with permission.

Figure 6. ***Fontinalis novae-angliae*** with underwater capsules, a species that can survive for one year above water if the desiccation is slow. Photo by Janice Glime.

Gupta (1977a) compared photosynthesis in the drought-resistant ***Porella platyphylla*** (a terrestrial epiphytic leafy liverwort; Figure 7) with the non-resistant ***Scapania undulata*** (a usually submersed stream liverwort; Figure 8). Using a relative humidity of 96.5% for various periods, he found the same pattern of variation in the relative water content during the water stress, dropping steadily for up to 50 hours, then remaining unchanged, presumably having reached an equilibrium with the atmosphere. Both species exhibited peak photosynthesis during the initial phase of water loss, then experienced a steady decrease as more water was lost. But it was the drought-resistant ***P. platyphylla*** that reached its photosynthetic peak sooner (2 hours) compared to ***S. undulata*** after 6 hours. **Desiccation avoidance** (the ability to conserve water and prevent desiccation) is not the same as **desiccation tolerance** (the ability to survive despite being desiccated). The reason for this difference is not clear. Could it be the ability to gain more CO_2 as it dries but still has enough water?

Figure 7. ***Porella platyphylla***, an epiphytic leafy liverwort that is drought resistant. Photo by Evan Raskin, through Creative Commons.

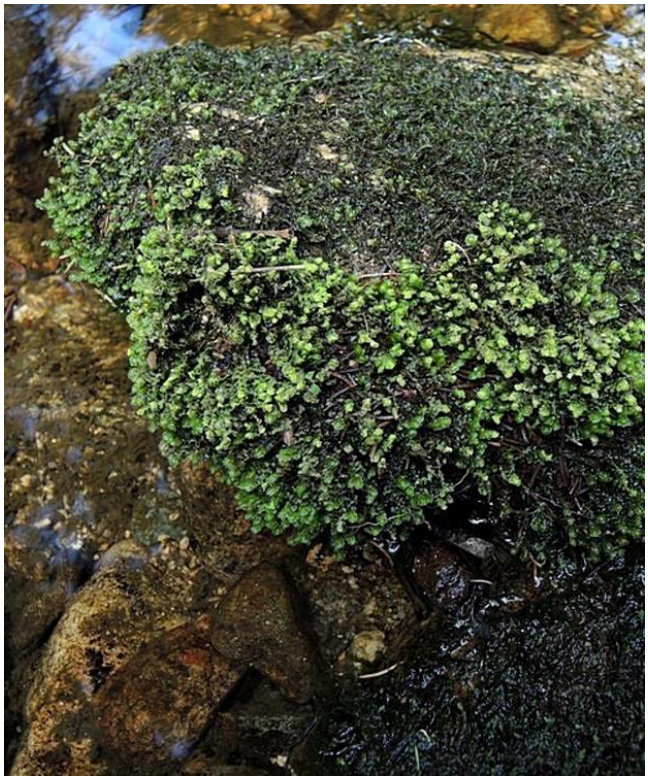

Figure 8. ***Scapania undulata***, an aquatic leafy liverwort that is non-resistant to the effects of desiccation. Photo by Michael Kesl, through Creative Commons.

Drying Effects

Tolerance of drying air differs by habitat (Johnson & Kokila 1970). For ten species of tropical mosses, two groups of resistance were evident. One group had high resistance to desiccation, and the other had low resistance. The high-resistance species occurred in niches with low humidity in the tropical forest. These mosses had high osmotic value and were able to absorb water vapor from the air. We should expect most aquatic bryophytes to fall into the second group.

Aquatic mosses grown out of water become pale in color (Davy de Virville 1927a, b; Henry 1929). These water-stressed mosses possess more numerous chloroplasts, but less chlorophyll, than those remaining submersed. These two researchers also report that some aquatic mosses, particularly ***Warnstorfia fluitans*** (often emergent; Figure 9), develop denser tissues when grown out of water (apparently meaning more, but smaller, cells). And the leaves also develop more denticulations in this species, but no denticulations were formed in ***Fontinalis novae-angliae*** (Figure 6) or ***F. dalecarlica*** (Figure 5), nor did the cells become more dense. It appears that species such as ***Warnstorfia fluitans*** that live partly in and partly out of the water may have more or different mechanisms for coping with lack of water.

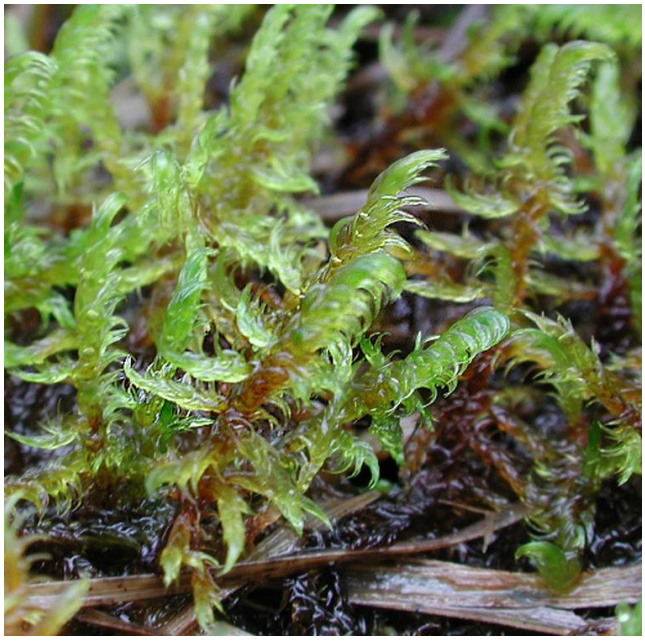

Figure 9. ***Warnstorfia fluitans*** growing emergent. Photo by Norbert Schnyder, with permission.

A further mechanism to survive desiccation is the ability of leaf fragments or torn leaves to produce protonemata. This is known in ***Platyhypnidium riparioides*** (Figure 10 (Elssmann 1923). As noted in subchapter 2-5, when Glime (1971) removed ***Fontinalis dalecarlica*** (Figure 5) and ***F. novae-angliae*** (Figure 6) from a New Hampshire, USA, stream and placed them on the stream bank, the stems, but not the leaves, survived for one year. These stems were able to subsequently grow new leaves when they were returned to the water of the streams. ***Fontinalis*** stems are more resistant than the leaves, and at least some members of this genus are able to produce protonemata from broken stems (Figure 11), further helping isolated plants to survive when returned to water (Glime 2014).

Figure 10. ***Platyhypnidium riparioides***, a species of submerged and emergent rocks. Photo by J. C. Schou, through Creative Commons.

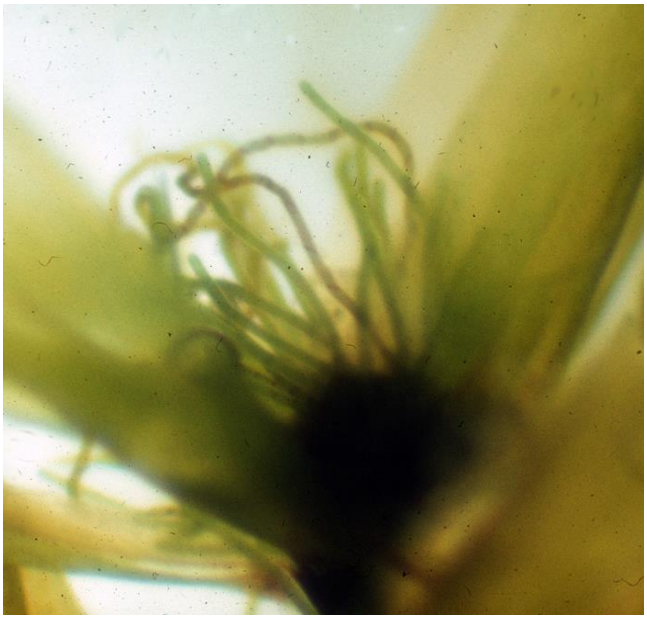

Figure 11. ***Fontinalis hypnoides*** regeneration, showing protonemata at broken stem tip. Photo by Janice Glime.

An early researcher, Schröder (1886), demonstrated the ability of bryophyte stems to be highly resistant to desiccation. Irmscher (1912) reported that leaves of air-dried ***Fontinalis antipyretica*** (Figure 4, Figure 12) and ***F. squamosa*** (Figure 1) died in only 7 days. Those in a desiccator died in 5 days. But he observed that both species produced numerous new sprouts when rewet. Irmscher demonstrated survival of ***Fontinalis*** stems after three weeks of desiccation (see for example Figure 13); these plants also produced new growth from the highly protected apical bud. On the other hand, leaves of ***Philonotis fontana*** (Figure 14), an emergent moss, remained healthy for 20 weeks when air-dried and 18 weeks in a desiccator.

Figure 12. ***Fontinalis antipyretica***, a species that dies after one week of lab drying with no preconditioning. Photo by Matt Goff at www.sitkanature.com, with permission.

Figure 13. ***Fontinalis antipyretica*** out of water, a common occurrence in small streams in summer. Photo by Andreas Rockstein, through Creative Commons.

Figure 14. ***Philonotis fontana*** at the edge of a stream where it is occasionally inundated. Photo by Janice Glime.

But since Irmscher (1912) made his observations, we have learned that rapid drying in the laboratory prevents bryophytes from preparing for desiccation (Gupta 1978b; Stark *et al*. 2013). On the other hand, in nature stream bryophytes typically remain moist for days following low water that leaves them stranded out of water (Figure 1).

Peñuelas (1984b) found that it took 1-4 weeks for bryophytes removed from stream water to the stream bank to show cellular damage. In similar experiments Glime (1971) found that when ***Fontinalis dalecarlica*** (Figure 5) and ***F. novae-angliae*** (Figure 6) were removed from the water to the stream bank in September and returned to the water from the same September to April, they restored their bright green leaf color within a few days. It is likely that they remained hydrated most of this time, either from autumn rain or snow cover.

Gupta (1978b) tested the effect of pretreatment by subjecting the mosses ***Calliergonella cuspidata*** (Figure 15), ***Fissidens adianthoides*** (Figure 16), and ***Fontinalis antipyretica*** (Figure 12), and the leafy liverwort ***Scapania undulata*** (Figure 8) to 98% humidity for 24 hours prior to reduction to 50% relative humidity. When this pretreatment occurred the plants lost much less water initially. He tested ***F. antipyretica*** for changes in water soluble proteins and found no increase. From this he concluded that the increase in resistance to desiccation was due to the change in rate of water loss rather than an effect on a physiological process. In these experiments, ***F. antipyretica*** had a much greater increase in desiccation resistance than did ***Scapania undulata***. The former is a fully submersed species that can be stranded above water at times of low flow. ***Scapania undulata*** often grows where it is subjected to water level fluctuations in step falls and on emergent but wet rocks, as well in locations with shallow submersion. It is possible that it was already naturally "pretreated."

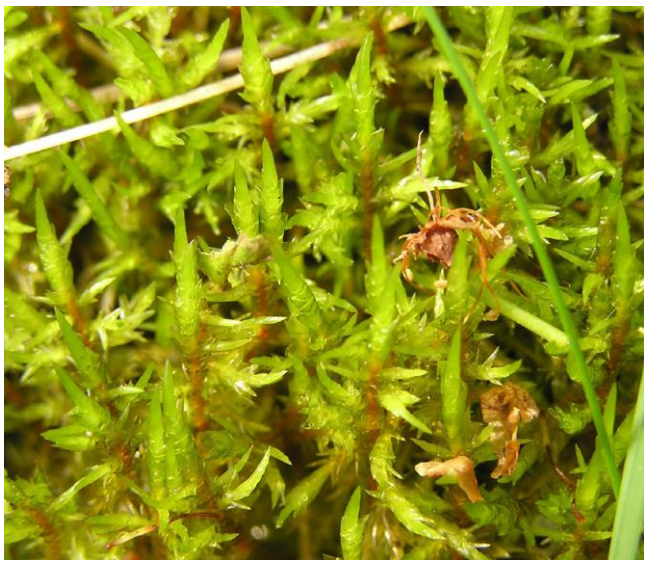

Figure 15. ***Calliergonella cuspidata***, an emergent species that survives desiccation when dried slowly, *i.e.* with pretreatment. Photo by Michael Becker, through Creative Commons.

Figure 16. ***Fissidens adianthoides*** with capsules. Photo by Bob Klips, with permission.

Even using the severe conditions of a lab, some emergent mosses [***Warnstorfia exannulata*** (Figure 17), ***Warnstorfia fluitans*** (Figure 18), ***Drepanocladus aduncus*** (Figure 19), and ***Philonotis fontana*** (Figure 14)] survived 15-20 weeks before dying (Irmscher 1912).

Figure 17. ***Warnstorfia exannulata***, an emergent species that can survive up to 15-20 weeks of drying. Photo by David T. Holyoak, with permission.

Figure 18. ***Warnstorfia fluitans***, an emergent species that can survive up to 15-20 weeks of drying. Photo by Michael Lüth, with permission.

Figure 19. ***Drepanocladus aduncus***, an emergent species that can survive up to 15-20 of drying. Photo by Bob Klips, with permission.

Fontinalis flaccida (Figure 20) from a lake bottom (about 1 m depth) survived drying as a herbarium specimen for three months, then resumed growth in an artificial stream (Glime & Vitt 1984). ***Fontinalis antipyretica*** (Figure 12) exhibited a desiccation threshold at 90% relative humidity, whereas ***F. squamosa*** (Figure 1) did not reach its threshold until 10% (Abel 1956). Abel suggested that hygrophytes have a primary desiccation threshold of 82% relative humidity, but habitats can be a major influence on that level.

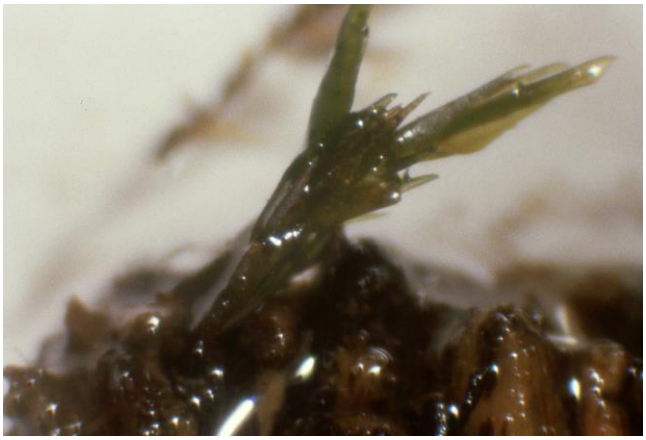

Figure 20. ***Fontinalis flaccida*** growing on limnephilid case at Tepee Lake, Michigan, USA. photo by Janice Glime.

Measurements of photosynthetic efficiency can help us understand some aspects of desiccation tolerance. Arscott *et al*. (2000) found that photosynthetic efficiency helped to explain the ability of ***Schistidium agassizii*** (=*S. alpicola*; Figure 21) to live in the river under cold, low-nutrient conditions, but ***Hygrohypnum alpestre*** (Figure 22) and ***H. ochraceum*** (Figure 23) could not. In the two ***Hygrohypnum*** species, respiration after 10 and 37 hours of rehydration were significantly lower than rates for those plants that had not been dehydrated. Desiccation effects on net photosynthesis in ***Schistidium agassizii*** were less dramatic and differed little from reference populations after 37 hours. On the other hand, ***Hygrohypnum*** species had greater tolerance of temperatures above 20ºC and significantly greater net photosynthetic rates at light saturation than did ***S. agassizii***.

Figure 21. ***Schistidium agassizii***, a wet rock species that has greater tolerance of desiccation than submersed species. Photo from Proyecto Musgo, with permission.

Figure 22. ***Hygrohypnum alpestre***, a species that is sensitive to desiccation. It is shown here with **pearling**, air bubbles produced by photosynthesis trapped among the leaves. Photo by Michael Lüth, with permission.

Figure 23. ***Hygrohypnum ochraceum***, a species that is sensitive to desiccation. Photo by S. H. Studdard, through Creative Commons.

Gupta (1978a) tested five bryophyte species for their desiccation tolerance. Of these, the aquatic liverwort ***Scapania undulata*** (Figure 8) had the least desiccation tolerance compared to the more terrestrial species. It lost water the fastest and had the greatest total loss after 8 hours compared to ***Syntrichia ruralis*** (Figure 24), ***Porella platyphylla*** (Figure 7), ***Mnium hornum*** (Figure 25), and ***Rhizomnium punctatum*** (Figure 26), all more terrestrial species. Both chlorophyll *a* and *b* were damaged by desiccation, with more damage to *a* than *b*.

Figure 24. ***Syntrichia ruralis***, a drought-tolerant species. Photo by Darkone, through Creative Commons.

Figure 25. ***Mnium hornum***, a forest floor drought-tolerant species. Photo by Bob Klips, with permission.

Figure 26. ***Rhizomnium punctatum***, a relatively drought-tolerant species often found on rocks in canyons. Photo by Hermann Schachner, through Creative Commons.

At least some aquatic moss cell walls appear to be adapted for the alternating wet and dry conditions (Roberts & Haring 1937). ***Fontinalis gigantea*** (Figure 27) has large quantities of pectic substances in its cell walls. These allow for rapid water intake. Cutin mixed with pectinaceous substances in the epidermis of the stems could account for water retention.

Figure 27. ***Fontinalis gigantea*** dry in a vernal pool. Photo by Janice Glime.

Cruz *et al*. (2008) used chlorophyll fluorescence as a measure of desiccation effects on the aquatic moss

Fontinalis antipyretica (Figure 4). These measurements were accompanied by O_2 evolution and ion leakage. There was considerable increase of O_2 consumption in the dark that was not inhibited by mitochondrial inhibitors. Photosynthetic activity suffered severe decreases under extreme desiccation and was unable to recover to its normal metabolic activity. Leakage of electrolytes indicated cellular membrane damage.

Membrane Leakage

One of the problems caused by desiccation is membrane leakage. This is most pronounced for soluble substances such as potassium (K). Deltoro *et al*. (1998) compared several bryophytes representing xeric [***Hedwigia ciliata*** (Figure 28), ***Hypnum cupressiforme*** (Figure 29), ***Leucodon sciuroides*** (Figure 30), ***Orthotrichum cupulatum*** (Figure 31), ***Pleurochaete squarrosa*** (Figure 32), ***Porella platyphylla*** (Figure 7), and ***Syntrichia ruralis*** (Figure 24)] as well as mesic, and hydric environments [***Barbula ehrenbergii*** (Figure 33), ***Cinclidotus aquaticus*** (Figure 34), ***Conocephalum conicum*** (Figure 35), ***Lunularia cruciata*** (Figure 36), ***Palustriella commutata*** (Figure 37), ***Philonotis calcarea*** (Figure 38), and ***Platyhypnidium riparioides*** (Figure 10)]. Deltoro and coworkers suggested that this lack of return to normal photosynthesis might be caused by **photoinhibition** (light-induced reduction in the photosynthetic capacity) or membrane damage. There was an accompanying large leakage of K. The leakage may have been exacerbated by more rapid than normal drying.

Figure 28. ***Hedwigia ciliata***, a xeric, rock-dwelling moss. Photo by Štěpán Koval, with permission.

Figure 29. ***Hypnum cupressiforme***, a relatively xeric moss. Photo by Kurt Stüber, through Creative Commons.

Figure 30. ***Leucodon sciuroides*** with capsules, a xeric moss. Photo by Hughes Tinguy, with permission.

Figure 31. ***Orthotrichum cupulatum*** with capsules, a xeric moss. Photo by Hermann Schachner, through Creative Commons.

Figure 32. ***Pleurochaete squarrosa*** dry, a xeric moss. Photo by David T. Holyoak, with permission.

Figure 33. ***Barbula ehrenbergii***, a species of hydric environments. Photo by Michael Lüth, with permission.

Figure 34. ***Cinclidotus aquaticus***, a species of hydric environments on emergent rocks. Photo by Hermann Schachner, with permission.

Figure 35. ***Conocephalum conicum***, a species of mesic to hydric environments. Photo by Hermann Schachner, through Creative Commons.

Figure 36. ***Lunularia cruciata***, a species of mesic environments. Photo from Botany Website, UBC, with permission.

Figure 37. ***Palustriella commutata***, a species of wet environments. Photo by Hermann Schachner, through Creative Commons.

Figure 38. ***Philonotis calcarea***, a species of wet environments. Photo by Hermann Schachner, through Creative Commons.

Gupta (1977b) found that maximum leakage occurred within the first two minutes of rewetting in the terrestrial ***Porella platyphylla*** (Figure 7), emergent ***Plagiochila asplenioides*** (Figure 39), terrestrial ***Plagiothecium undulatum*** (Figure 40), and aquatic ***Scapania undulata*** (Figure 8). After that, the leakage rate slowed down. Gupta suggested that this slowing is due to the reassemblage of the membrane structures or to the rapid decrease of solutes within the injured and dead tissues. All of these species occur in habitats with a wide range of moisture stress. If the solutes are not washed away, they can be reabsorbed by living cells.

Figure 39. ***Plagiochila asplenioides***, a species that exhibits one of the high levels of solute leakage in the first two minutes of rehydration. Photo by Hermann Schachner, through Creative Commons.

Gupta (1979) used tracers to determine the loss of leachates from the aquatic leafy liverwort ***Scapania undulata*** (Figure 8) during desiccation after pretreatment at 96% relative humidity for 48 hours. In this species 7 carbohydrates, 13 amino acids, and 3 organic acids were identified in the leachates. There appeared to be little selectivity in what was lost, and the leakage appeared to be simple diffusion. Nevertheless, the amino acids threonine, methionine, and valine were not detected in the leachate.

Figure 40. ***Plagiothecium undulatum***, a species that exhibits the most solute leakage among four species tested in the first two minutes of rehydration. Photo by David T. Holyoak, with permission.

Rate of Drying

But in many early studies, the question of rate of drying had not been considered. As early as 1990, Proctor recognized the importance of drought-hardening as the bryophyte dries. Growth form is a strong influence on both rate of drying and the ability to rehydrate when water becomes available. The growth form contributes to the boundary-layer resistance, a factor that is critically important in determining water loss.

Carvalho (2009) noted that whereas many studies exist on desiccation effects on terrestrial bryophytes, few exist for aquatic species. To help us understand some of the differences between terrestrial and aquatic bryophyte strategies, Carvalho desiccated ***Fontinalis antipyretica*** (Figure 12) at different relative humidities, then rapidly rehydrated them. The desiccation stress caused membrane damage. This, in turn, resulted in decreases in gross photosynthesis and the maximum photochemical efficiency of PSII (Fv/Fm). Rehydration resulted in a strong respiratory burst (ca 1200 µmol O_2 g^{-1} DW h^{-1}).

Krochko *et al*. (1979) noted that oxygen consumption increased considerably during the latter stages of desiccation in both the desiccation-tolerant ***Syntrichia ruralis*** (Figure 24) and the desiccation-intolerant ***Cratoneuron filicinum*** (Figure 41). The ATP content was influenced not by the O_2 consumption, but by the rate of drying. The more rapidly the mosses dried, the more ATP was present in the dry mosses. When the mosses were rehydrated, the rate of O_2 consumption in ***S. ruralis*** was considerably elevated for up to 24 hours after rapid desiccation, but the elevation was small and endured for only a brief time after slow desiccation. In ***C. filicinum***, normal O_2 consumption did not return following rapid dehydration, but returned within a few hours following slow desiccation. In ***S. ruralis***, normal ATP levels returned within 5-10 minutes of rehydration. In ***C. filicinum***, the increases in ATP closely followed the O_2 consumption. The researchers suggested that the differences between the

species might relate to the ability to repair cellular damage after rapid desiccation.

Figure 41. ***Cratoneuron filicinum***, a desiccation-intolerant species of wet areas. Photo by David T. Holyoak, with permission.

Recovery

I once dried ***Fontinalis flaccida*** (Figure 20) on index cards in the lab where air can be quite dry. After it stayed more than a month in that state, I put it in an experiment to determine the effects of flowing water on the stem structure, and hoped. Fortunately, it grew in the experiment!

One important difference is in recovery rate between terrestrial and aquatic species (Carvalho 2009). In the widespread aquatic moss ***Fontinalis antipyretica*** (Figure 12), H_2O_2 production increased immediately in the tips upon rehydration. This production increased when the relative water content was decreased, and production slowly decreased during the next 25 minutes of rehydration. Recovery of photosynthesis and respiration was slow over a five-day period and was even slower at lower relative water contents or when the desiccation rate was faster. Full photosynthesis and respiration had not yet returned after five days. It is interesting that the amount of water lost has a greater effect on membrane integrity and photosynthesis than does the rate of water loss. Nevertheless, a greater rate of water loss can exacerbate the stress effects of water loss. This suggested that rapid water loss did not allow sufficient time for activation of protective mechanisms against desiccation.

In their desiccation experiments with ***Fontinalis antipyretica*** (Figure 12), Carvalho *et al*. (2011) found that slow drying is necessary for the moss to recover fully. On the other hand, the extent of dehydration influences metabolism. In 2013, Carvalho followed up on these observations, concluding that desiccation tolerance in ***Fontinalis antipyretica*** (Figure 12) is determined by the extent of dehydration, the rate at which it occurs, or by both. The rehydration behavior of this species indicates that it is desiccation tolerant, a property that permits it to survive in waterways that dry up for part of the year. Oxidative stress is associated with survival of desiccation; this species experiences an increase in reactive oxygen species production due to metabolic impairment resulting from dehydration. The reactive oxygen species production was very high under rapid dehydration, but almost nonexistent under slow dehydration. This highly reactive oxygen reacts with such cellular constituents as proteins and lipids, causing damage to the cell.

Photoinhibition

Deltoro *et al*. (1998) found that at low water content, fluorescence characters indicated low efficiency of photosynthetic quantum conversion, closed PS II reaction centers, and strong nonphotochemical quenching only in those species known to be desiccation tolerant. Upon rehydration, return of fluorescence indicated that the photosynthetic apparatus had returned to full function. However, for those species from hydric and mesic habitats, photochemical activity did not return to normal. The researchers suggested that an increase in dissipation of thermal energy during dehydration might adapt xeric mosses to their erratic water supplies by lowering the potential for photodamage during water loss and early hydration, permitting the photosynthetic apparatus to recover quickly.

Supporting the suggestions of Deltoro *et al*. (1998), Carvalho *et al*. (2011, 2012) found that in ***Fontinalis antipyretica*** (Figure 12) PS II (PSII) regulation and structural maintenance are an important part of this induced desiccation tolerance mechanism that permits this moss to recover when it is dried slowly, as it would be in a drying stream bed. A decrease in the photochemical quenching coefficient (qP) immediately following rehydration may be important in alleviating the effects of excess energy on PS I (PSI) before the cells are fully functional, while low-level nonphotochemical quenching (NPQ) would allow an energy shift that enables recovery following extended periods of desiccation.

Sucrose Accumulation

During dehydration, sucrose can accumulate, changing the osmotic relationships (Carvalho 2013; Carvalho *et al*. 2014). Sucrose is important in desiccation tolerance through the prevention of macromolecule denaturation and the slowing of damaging reactions with the reactive oxygen species. Under fast dehydration, the characteristics of the cell walls change, permitting greater elasticity of the cytoskeleton. Hence, the bryophytes use a constitutive protection that permits tolerance of desiccation by protecting structural integrity. There is a reduction of proteins involved in photosynthesis and cytoskeleton structure, whereas those associated with sugar metabolism and plant defense increase. Then they use a repair-based mechanism upon rehydration to repair the damage of dehydration. This involves an accumulation of normal protein values for both photosynthesis and cytoskeleton while those proteins involved in sugar metabolism and

defense remain light. This repair mechanism is activated by the accumulation of mRNA during rehydration. When the plants are dried rapidly, they lose nearly all proteins; this is not the case under slow drying. This supports the hypothesis that slow-drying is necessary to manufacture protective proteins. In short, desiccation-tolerance responses of aquatic bryophytes like ***Fontinalis antipyretica*** (Figure 12) appear to be the same as those of desiccation tolerant terrestrial bryophytes.

More Leakage Problems

Despite the protections of slow drying, dry membranes leak electrolytes (Carvalho *et al*. 2015). In terrestrial mosses, rehydration is typically slow, permitting the cells to reabsorb lost minerals and nutrients in the first few minutes of rainfall before they can be washed away. This may not be the case in aquatic systems where water can return suddenly from an upstream source. Slow dehydration permits the cell wall to gain elasticity, but rapid dehydration results in a higher sucrose accumulation. Sugar acts as an osmolyte in bryophytes, while stabilizing membranes and proteins through vitrification. But after rapid dehydration, leaves lose 50% of their accumulated sucrose through leakage. The result is that the sucrose is insufficient to establish desiccation tolerance. Life forms may help some species slow dehydration, providing another protective measure. Carvalho *et al*. noted that in ***Fontinalis antipyretica*** (Figure 12) the growth form permits the plants to create numerous capillary spaces where water is held, permitting slow drying.

Gupta (1976) reported the leakage of 15 amino acids from ***Plagiochila asplenioides*** (Figure 39) following desiccation for 48 hours at 50% relative humidity, and rehydration. This was accompanied by the loss of 3 unknown compounds, nearly 10 carbohydrates, and 4 organic acids. He found that practically all the soluble compounds in the plant shoots were able to leak out during this dehydration-rehydration protocol, most likely through passive diffusion through leaky membranes.

Invaders in the Mix

Leakage from the cell indicates that there are holes in the cell membranes. That could make it possible for invading microbes to enter the cells, making new food supplies available to them, and perhaps more importantly, organic leakage providing food outside the cell, the latter demonstrated by Gupta (1977c). Gupta found that the burst of respiration following desiccation and rehydration was not a function of the cell, but rather increased respiration by the microbes that had gained more favorable conditions. This burst of respiration was exhibited on xerophytic [***Syntrichia ruralis*** (Figure 24; no significant change); ***Porella platyphylla*** (Figure 7) (2X)], mesophytic [***Mnium hornum*** (Figure 25; 2X)], meso- to hydrophytic [***Dichodontium palustre*** (Figure 42; 2.5X)], and hydrophytic [***Scapania undulata*** (Figure 8; 6X)] bryophytes.

Figure 42. ***Dichodontium palustre***, a species that may be submersed or in the splash zone. Photo by Hermann Schachner, through Creative Commons.

Polyribosomes and Protein Synthesis

Bewley (1974) found that when the aquatic moss ***Hygrohypnum luridum*** [Figure 43; probably ***Cratoneuron filicinum*** (Figure 41), as identified later] was desiccated, it did not matter if it was done quickly or slowly in a saturated atmosphere. Both of these conditions caused an irreversible loss of polyribosomes. Furthermore, the moss was unable to recover and resume protein synthesis when it was rehydrated. This is in contrast to the sequence of events and recovery in the drought-tolerant terrestrial moss ***Syntrichia ruralis*** (Figure 24).

Figure 43. ***Hygrohypnum luridum***, a moss on emergent rocks. Photo by Andrew Melton, through Creative Commons.

Gwozdz and Bewley (1975) considered the effects of fast and slow drying on ***Syntrichia ruralis*** (Figure 24) and its retention of polyribosomes. This desiccation-tolerant moss actually retained fewer polyribosomes when dried slowly, the ribosomes were more active than in the rapidly dried moss. The major protein synthesis occurs in the cytoplasm on rehydration. Hence, in the slowly dried mosses, this retention of synthetic capacities permits them

to resume protein synthesis more quickly than in rapidly dried mosses. They found that the aquatic moss ***Hygrohypnum luridum*** [Figure 43; probably the moss later identified as ***Cratoneuron filicinum*** (Figure 41)] retained its polyribosomal and ribosomal activity during desiccation, but suffered great loss of activity on rehydration.

Non-autotrophic CO_2 Fixation

Not all CO_2 is fixed into carbohydrates for structure or storage. CO_2 fixation can also occur in the dark and is incorporated into amino acids (> 60% of total, mainly into aspartate, alanine, and glutamate) and organic acids (< 40%). ***Cratoneuron filicinum*** (Figure 41), a drought-sensitive species, and ***Syntrichia ruralis*** (Figure 24), a drought-tolerant species, fix CO_2 non-autotrophically at a rate of about 1.2 and 2.2 µmol h^{-1} g^{-1} dry weight, respectively (Dhindsa 1985). During drying these two species differ in their responses. The dark CO_2 fixation rate of ***S. ruralis*** does not diminish until the tissues lose about 60% of their original fresh weight. This dark fixation resumes immediately upon rehydration in this species, but not in ***C. filicinum***. Nevertheless, even in ***S. ruralis***, when dry plants are placed in nearly 100% relative humidity, the weight increases to only about 40% of the original hydrated weight and dark CO_2 fixation returns to only about 60% of that in the fresh moss. Dhindsa suggested that the immediate availability of NADPH, produced from NADH during dark CO_2 fixation, in drought-tolerant species may be important in repairing cellular damage through reductive biosynthesis of membrane components and other damaged cellular constituents.

Temperature Effects

Chlorophyll content can serve as a surrogate for cell health. Hearnshaw and Proctor (1982) used chlorophyll content to determine the loss of viability in seven species [***Anomodon viticulosus*** (Figure 44), ***Racomitrium aquaticum*** (Figure 45), ***R. lanuginosum*** (Figure 46), ***Tortella humilis*** (Figure 47), ***Andreaea rothii*** (Figure 48), ***Frullania tamarisci*** (Figure 49), and ***Porella platyphylla*** (Figure 7)] of bryophytes that were kept dry at temperatures ranging 20-100ºC from a few minutes to weeks or months. Although the different temperatures tended to affect all of them similarly, the time required for the same amount of damage differed widely. At 100ºC, the least resistant species suffered a 50% loss of chlorophyll in a few minutes or less. The more resistant species survived at 20 and 37ºC for weeks to months before experiencing 50% chlorophyll loss. Both ***Racomitrium*** species exhibited great tolerance at temperatures in the middle part of the range investigated, despite ***R. aquaticum*** occurring on moist, shaded rocks and ***R. lanuginosum*** occurring frequently in the tundra and tropical alpine areas, although these locations are frequently misty or humid.

Figure 44. ***Anomodon viticulosus***, a xeric species. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Racomitrium aquaticum***, a species of wet habitats. Photo by Hugues Tinguy, through Creative Commons.

Figure 46. ***Racomitrium lanuginosum***, a xeric moss. Photo by Hermann Schachner, through Creative Commons.

Figure 47. ***Tortella humilis***, a species of rock crevices near water. Photo by Bob Klips, with permission.

Figure 48. ***Andreaea rothii***, a rock-dwelling xeric moss. Photo by David T. Holyoak, with permission.

Figure 49. ***Frullania tamarisci***, a moss that can be exposed to a wide range of humidities. Photo by Tim Waters, through Creative Commons.

Pigment Responses

Like **e**migration and **im**migration, **emersion** is the process of exiting and **immersion** is the process of entering the water. These two processes affect mosses from different habitats differently. Peñuelas (1984b) found that aquatic moss species lost 50% of their chlorophyll in very few weeks of emersion, with pigments having OD430/OD665 being most sensitive. The phaeo-pigment proportion was sensitive to periods of rainfall and humidity. ***Cinclidotus fontinaloides*** (Figure 50) was the most tolerant species, ***Fontinalis antipyretica*** (Figure 12) the least. By contrast, all terrestrial mosses studied lost 50% of their chlorophyll content in the first week of immersion. Spitale (2009) even found that he could use pigments as indicators of the height above the water table, hence the moisture conditions, in spring systems.

Figure 50. ***Cinclidotus fontinaloides***, a species of emergent rocks that is relatively tolerant of desiccation. Photo by Hermann Schachner, through Creative Commons.

Fatty Acid Responses

Stewart and Bewley (1982) found that both the desiccation tolerant ***Syntrichia ruralis*** (Figure 24) and the desiccation-intolerant ***Cratoneuron filicinum*** (Figure 41) maintained their fatty acid phospholipid composition during rapid drying. However, after slow drying, some unsaturated fatty acids decline. After slow drying, ***S. ruralis*** exhibits further decline of these fatty acids upon rehydration. Then, after ~105 minutes, they regain their original nondesiccated levels. After rapid desiccation, the decline is smaller and more transient. On the other hand, in ***C. filicinum*** most of the phospholipid unsaturated fatty acids decrease during rehydration, and these are never recovered. In contrast to ***S. ruralis***, ***C. filicinum*** exhibits very little incorporation of acetate or glycerol during rehydration.

Fatty acid concentrations vary widely among the bryophytes (Dembitsky & Rezanka 1995). For example, acetylenic fatty acid concentration in the wetland moss ***Calliergon cordifolium*** (Figure 51) was 6.6% but reached 80.2% in the floating thallose liverwort ***Riccia fluitans***. At the very least, these differences suggest that we need to look at the role of fatty acids as protective substances in bryophytes.

Figure 51. ***Calliergon cordifolium***; the genus ***Calliergon*** has algal fatty acids. Photo by Jerry Jenkins, Northern Forest Atlas, with permission.

ABA Mediation

Noting the ancestral terrestrial life style of bryophytes and their evolutionary history of going back and forth between terrestrial and aquatic environments, Wanke (2011) explored the role of the hormone ABA in submersed-emersed switches. This environmentally responsive hormone has been present throughout the plant kingdom from bryophytes to flowering plants. It can initiate the production of other hormones.

Whereas **heterophylly** (having more than one leaf type on same plant) is common between submersed and emergent leaves of tracheophytes, such heterophylly is rare among bryophytes. In the tracheophyte *Callitriche heterophylla*, **GA** (gibberellic acid, a growth hormone) induces cell elongation, causing emergent leaves to resemble submersed leaves (Deschamp & Cooke 1985). On the other hand, GA seems to induce **heterophylly** through a pathway with the gaseous hormone **ethylene**, and this antagonizes the synthesis of the hormone **ABA**. Thus, when aerial shoots of *Ludwigia arcuata* (Figure 52) were exposed to ethylene, they were induced to form leaves resembling submersed leaf morphology (Kuwabara *et al*. 2003; Kuwabara & Nagata 2006). Little work has been done with bryophytes and the effects of these three hormones. Yet we know that ACC, the ethylene precursor, has a significant effect on morphology and coloration in ***Fontinalis squamosa*** (Figure 1) and ***F. antipyretica*** (Figure 12) (Glime & Rohwer 1983). We need to investigate its role in emergent vs submergent morphology.

Figure 52. ***Ludwigia arcuata***, an aquatic tracheophyte that responds to ethylene concentrations to determine leaf shape. Photo by Shaun Winterton, through Creative Commons.

Added ABA in three bryophytes [mosses ***Physcomitrella patens*** (Figure 53) and ***Atrichum undulatum*** (Figure 54) and liverwort ***Marchantia polymorpha*** (Figure 55)] caused these bryophytes to exhibit a decrease in total chlorophyll and carotenoids (Vujičić *et al*. 2016). Effects on growth were unclear. It is likely that ABA has effects on desiccation tolerance in aquatic bryophytes, but much more research is needed to understand the role of this hormone in bryophytes.

Figure 53. ***Physcomitrella patens***, a moss that responds to added ABA by a reduction in total chlorophyll. Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Atrichum undulatum***, a moss that responds to added ABA by a reduction in total chlorophyll. Photo by David T. Holyoak, with permission.

Figure 55. ***Marchantia polymorpha*** with gemmae cups, a liverwort that responds to added ABA by a reduction in total chlorophyll. Photo by Hermann Schachner, through Creative Commons.

Allocation Changes

Rice (1995) compared allocation and growth in pairs of aquatic and non-submersed species of ***Sphagnum*** (Figure 56-Figure 58). The submerged taxa all had greater relative growth rates and greater allocation to their photosynthetic tissues (Figure 59) when compared to the non-aquatic species (Figure 60). The latter was expressed as higher whole plant chlorophyll content. In this genus, the greater allocation to photosynthetic processes was accomplished by fewer or smaller hyaline cells and a shift in the biochemical partitioning within the photosynthetic cells to favor light-reaction proteins. This latter factor was estimated from chlorophyll to nitrogen ratios. But these adaptations differed by species.

Figure 56. ***Sphagnum trinitense***, an aquatic species, paired with ***S. recurvum*** in the experiments by Rice (1995). Photo by Blanka Aguero, with permission.

Figure 57. ***Sphagnum recurvum***, a non-submersed species, paired with ***S. trinitense*** in the experiments by Rice (1995). Photo by Malcolm Storey, DiscoverLife.org, with online permission.

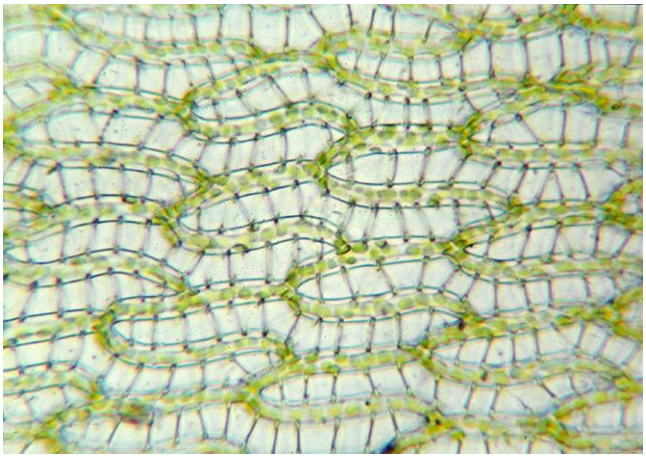

Figure 58. ***Sphagnum recurvum*** leaf cells, a non-submersed species, paired with ***S. trinitense*** in the experiments by Rice (1995). The less dense chlorophyll content and large hyaline cells are demonstrated in this non-aquatic species. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

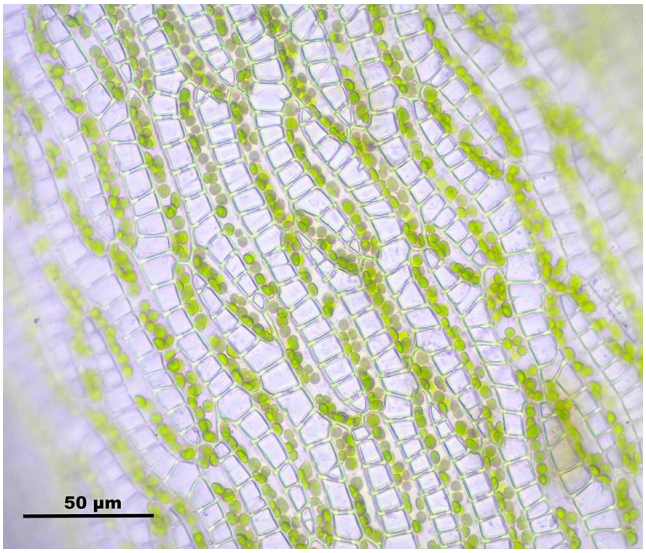

Figure 59. ***Sphagnum cuspidatum***, an aquatic species, showing small hyaline cells and dense chloroplasts in the photosynthetic cells. Photo by Hermann Schachner, through Creative Commons.

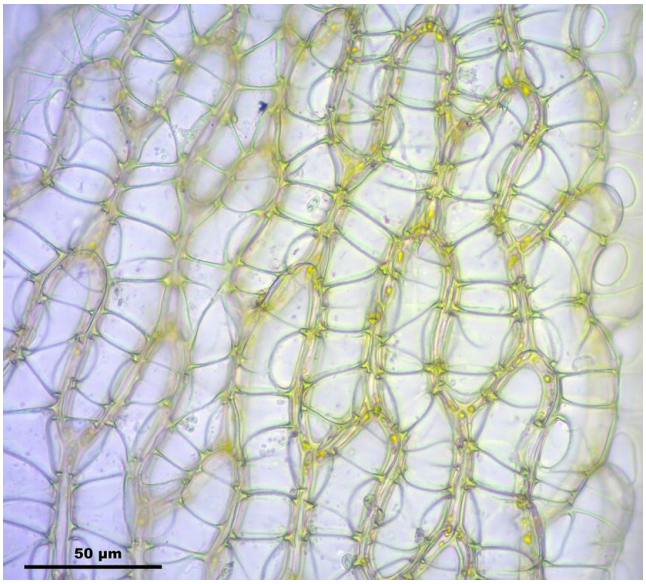

Figure 60. ***Sphagnum fuscum***, a hummock species, with leaf cells that show large hyaline cells that envelope the photosynthetic cells. Photo by Hermann Schachner, through Creative Commons.

Light

Proctor (1990) considered most bryophytes to be shade plants, having low chlorophyll *a*/*b* ratios, and reaching light saturation at relatively low light levels. They behave as C_3 plants, despite their ability to dry out to water contents as low as 5-10% of their dry weight. Growth forms can have a profound effect on the ability for light capture. Proctor stated that "bryophyte growth-forms must represent an adaptive balance between water economy and needs for light capture and carbon and mineral nutrient acquisition."

Most bryophytes seem unable to tolerate high light intensities. Aquatic bryophytes are typically protected from light by water depth, and in woodland streams and small pools, also by canopy cover. At cool temperatures, high light can cause severe reactions in ***Fontinalis antipyretica*** (Figure 12), resulting in loss of chlorophyll or production of bright red pigments (Figure 61-Figure 63) (Glime 1984).

Figure 61. ***Fontinalis antipyretica*** red (especially upper middle) in cold water and high light 15 May 1982 near Rothenfels, Germany. Photo by Janice Glime.

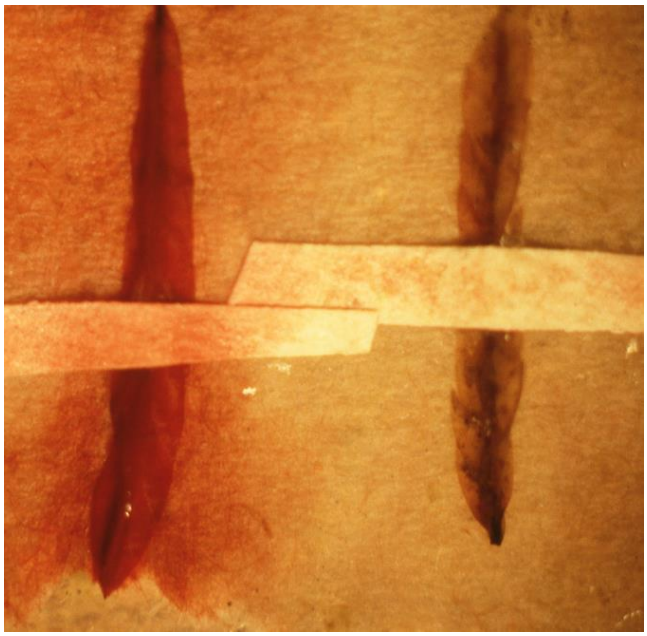

Figure 62. ***Fontinalis antipyretica*** red leakage in tropism experiment out of water, a response also seen in high light. Photo by Janice Glime.

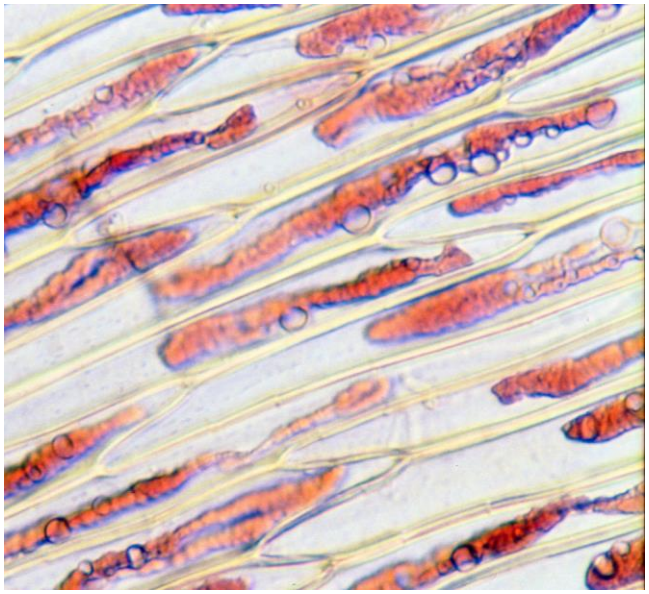

Figure 63. ***Fontinalis antipyretica*** red cells in tropism experiment out of water, a response similar to that in high light. Photo by Janice Glime.

Martin and Churchill (1982) found that both chlorophyll concentrations and *a*:*b* ratios were lower in bryophytes than for most tracheophytes. Those mosses collected from habitats with low light levels had higher chlorophyll concentrations and lower chl *a*:*b* ratios than those collected from high light levels. These differences suggest that changes in chlorophyll concentrations can adapt bryophytes to low or high light. Thus, we should expect mosses in forest streams to contain more chlorophyll than those in terrestrial habitats.

Bryophytes may have relatively low light optima. Using populations from the Keweenaw Peninsula of Michigan, USA, Glime and Acton (1979) found that the ***Fontinalis duriaei***-periphyton association had its maximum productivity at 10ºC, 5400 lux. At 5400 lux it approached light saturation under the experimental conditions, whereas direct sunlight at noon can reach 120,000 lux (Wikipedia 2019).

The ability to survive with low growth rates in low light permits bryophytes to live at depths of water that are unavailable to their tracheophyte competitors. For example, Westlake and Dawson (1976) noted that ***Fontinalis antipyretica*** (Figure 12) became a significant part of the plant biomass at depths greater than 1 m in the River Frome. Light there is only 30% of incident light.

Burr (1941) concluded that ***Fontinalis*** (Figure 5, Figure 6, Figure 12, Figure 20) reaches its light compensation at 150 lux at 20ºC and at 40 lux at 5ºC. Nevertheless, some species are tolerant of high light, such as ***Schistidium agassizii*** (Figure 21) in Alaskan streams (Bowden *et al*. 1994) and others (Ormerod *et al*. 1994).

Marschall and Proctor (2004) concluded that, based on 39 species of mosses and 16 of liverworts, bryophytes are generally shade plants. This was supported by total chlorophyll, Chl *a*:*b* ratio, PPFD values at 95% saturation mostly <1000 µmol m-2 s-1, but bryophytes in general "are not inherently shade plants." They concluded that their low productivity in the sun, relative to tracheophytes, was most likely limited by CO_2 diffusion into the leaves. The greater area with ventilated photosynthetic tissue (Figure 64), such as that of ***Polytrichum*** (Figure 65), may account for the greater productivity of members of that genus.

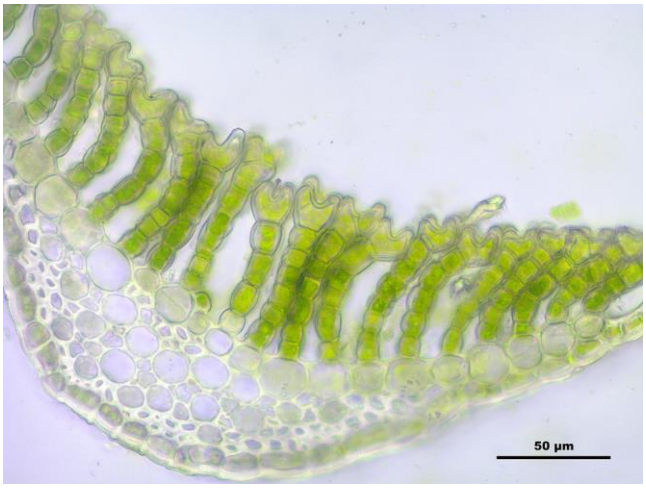

Figure 64. ***Polytrichum commune*** leaf cs showing the lamellae that create "ventilation" within the photosynthetic tissue. Photo by Hermann Schachner, through Creative Commons.

Figure 65. ***Polytrichum commune***, a wetland species with greater productivity than most mosses, perhaps due to its ventilated photosynthetic tissue. Photo by Michael Lüth, with permission.

López and Carballeira (1989) found that the aquatic mosses ***Fontinalis antipyretica*** (Figure 12), ***Brachythecium rivulare*** (Figure 66), ***Fissidens polyphyllus*** (Figure 67), ***Platyhypnidium riparioides*** (Figure 10), and the leafy liverwort ***Scapania undulata*** (Figure 8) exhibited a higher chlorophyll concentration than some terrestrial bryophytes. In addition to responses to low light, chlorophyll content responded to both organic and metal pollution. In this regard, ***Fontinalis antipyretica*** was the most resistant and ***Scapania undulata*** the most sensitive among these species.

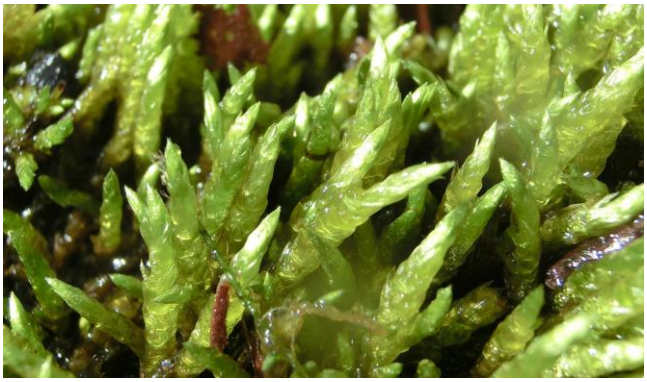

Figure 66. ***Brachythecium rivulare***, a wet habitat or emergent species with a higher chlorophyll content than most terrestrial bryophyte species. Photo by Michael Lüth, with permission.

Figure 67. ***Fissidens polyphyllus***, a species of wet cave walls and other wet habitats; it has a higher chlorophyll content than most terrestrial bryophyte species. Photo by David T. Holyoak, with permission.

Habitat Differences

Szarek (1994) found that other abiotic factors affected the chlorophyll *a* concentrations in mosses (and attached algae) in the Sucha Woda stream in the High Tatra Mountains of southern Poland. The lowest chlorophyll *a* concentrations were found in the high mountain part of the stream, whereas the lowest were found in the middle part. In that middle portion, significant differences in light intensity did not have any significant effect on the chlorophyll *a* content, suggesting that other factors were involved.

In the Kuparuk River of Alaska, USA, ***Schistidium agassizii*** (=***Schistidium alpicola***; Figure 21) exhibited little response to increases in light availability (Arscott *et al.* 2000). ***Hygrohypnum*** species (Figure 22, Figure 23, Figure 43), on the other hand, responded strongly to increases in light, helping to explain the distribution of these species in the Arctic.

In many locations, bryophytes are able to grow near lights in caves where the public have access. These are mostly terrestrial bryophytes growing on the walls of the caves. However, Thatcher (1949) found several typically aquatic or emergent mosses in Crystal Cave, Wisconsin, USA. Light where bryophytes grew ranged 269-9149 lux. Although Thatcher did not mention submersion for these species, the limestone cave supported the growth of ***Bryoerythrophyllum recurvirostrum*** (Figure 68), ***Leptodictyum riparium*** (Figure 69), ***Warnstorfia fluitans*** (Figure 18), and ***Brachythecium populeum*** (Figure 70), all of which can be submersed, as well as a number of terrestrial species. All of these "aquatic" species were new records for caves.

Figure 68. ***Bryoerythrophyllum recurvirostrum***, a basophile that can occur in limestone caves. Photo by Will Van Hemessen, through Creative Commons.

Figure 69. ***Leptodictyum riparium***, an aquatic moss that can occur in limestone caves. Photo by Hermann Schachner, through Creative Commons.

Patterson (1946) examined the osmotic values of bryophytes from different habitats, including a number of aquatic species, and found that these were correlated with the light intensity and not with the available moisture. The first and most typical of the behavior types was for species that became plasmolyzed at the same value after a dry period as when tested after a prolonged moist period. The second type was somewhat refractory toward plasmolyzing agents after a dry period and plasmolyzed at a somewhat

greater concentration than when tested after a moist period. A third type exhibited a marked temporary increase of its refractory property. A fourth type failed to plasmolyze at any time after a dry period – a response that was at one time considered to be true of all bryophytes. A fifth type exhibited aberrant behavior, with the same specimen sometimes becoming plasmolyzed and at others failing to do so, suggesting that some sort of preconditioning could be involved.

Figure 70. ***Brachythecium populeum*** with capsules, a moss that lives on emergent rocks and that can occur in limestone caves. Photo by Hermann Schachner, through Creative Commons.

Chlorophyll and Accessory Pigments

The aquatic bryophytes generally have the same pigments as the green algae and tracheophytes (Martínez-Abaigar & Núñez-Olivera 1998). In general, bryophytes have chlorophylls *a* and *b*, typically 24 carotenoids, including the pure hydrocarbons α and β carotene and the oxygen-containing xanthophylls lutein, zeaxanthin, violaxanthin, and neoxanthin as the most frequent (Taylor *et al* 1972; Schmidt-Stohn 1977; Czeczuga 1980, 1985; Czeczuga *et al.* 1982; Huneck 1983; Farmer *et al*. 1988; Boston *et al*. 1991). ***Fontinalis antipyretica*** (Figure 12) is unusual in having **auroxanthin** (Bendz *et al*. 1968), but otherwise there is no "outstanding" difference between terrestrial and aquatic bryophytes (Martínez-Abaigar & Núñez-Olivera 1998).

As is often the case, the nature or nurture question is not a yes or no comparison. Both are important. The pigment composition of bryophytes, including that of aquatic bryophytes, is a product of both genetic and environmental factors (Martínez-Abaigar & Núñez-Olivera 1998). At that time, we knew little about the anatomical factors or physiological factors that permitted bryophytes to survive high light intensities, especially among aquatic bryophytes. Nevertheless, some factors seemed to be characteristic. Researchers have warned that it is important to use the tips of the bryophytes where the highest chlorophyll contents occur (Schmidt-Stohn 1977; Martínez-Abaigar & Núñez-Olivera 1998).

Water effectively filters out red light, increasing with depth, leaving predominantly green light, but also blue (Kirk 1994) to penetrate to greater depths. Green light causes an increase in chlorophylls and carotenoids in ***Fontinalis*** (Figure 5, Figure 6, Figure 12, Figure 20) (Czeczuga 1987). Evans *et al*. (1974) recognized the importance of light as an ecological factor, examining such bryophytes as ***Fontinalis antipyretica*** (Figure 12) and ***Pellia epiphylla*** (Figure 71). Potential pigments to facilitate photosynthesis in lakes and other deep-water habitats are present in ***Bryum pseudotriquetrum*** (Figure 72) from Pletwicki Lakes, Yugoslavia (Czeczuga 1971). These include the carotenoids α-carotene, cryptoxanthin, lutein (epoxy and free), zeaxanthin, violaxanthin, and neoxanthin.

Figure 71. ***Pellia epiphylla***, a stream bank species. Photo by David T. Holyoak, with permission.

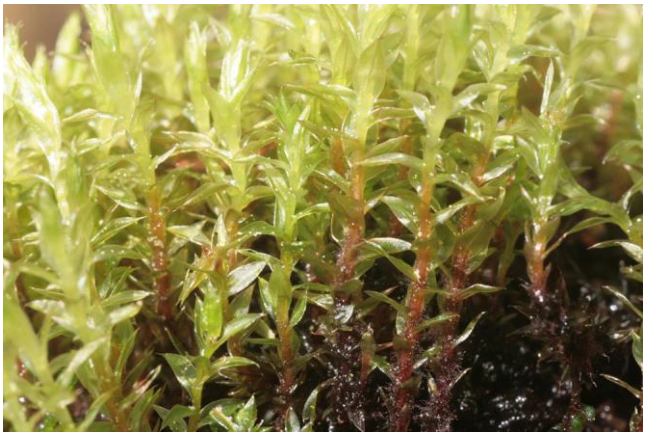

Figure 72. ***Bryum pseudotriquetrum***, a wetland species. Photo by Hermann Schachner, through Creative Commons.

Aquatic bryophytes have lower chlorophyll concentrations than do aquatic tracheophytes (Martínez-Abaigar & Núñez-Olivera 1998). Even the stream algae tend to have more chlorophyll than the bryophytes. The chlorophyll *b* and carotenoids serve as accessory pigments to capture the blue and green light and transfer it to the chlorophyll *a* action centers in the bryophytes (and other plants and algae). The chlorophyll *a*:*b* ratios of aquatic bryophytes typically range between 2 and 3 (Peñuelas

1984a, b; Peñuelas *et al* 1988; López & Carballeira 1989; Martínez-Abaigar *et al.* 1994). Tracheophytes typically have values between 2.4 and 3.7 (Martin & Churchill 1982). **Phaeophytins** may be produced as a result of stress that results in chlorophyll breakdown, but not all phaeophytin pigments are the result of breakdown.

Photosynthetic pigment concentrations change with the seasons (Martínez-Abaigar *et al*. 1994). These researchers analyzed pigment composition in 13 aquatic bryophytes from a variety of habitats. Chlorophyll content ranged 2.2-9.2 mg g^{-1} dry weight, 97-351 mg m^{-2} shoot area. These values were higher than those reported in terrestrial bryophytes, but lower than in tracheophytes. They were similar to those of epilithic river algae. Chlorophyll *a*/*b* ratios (2.1-2.8) and carotenoid indices of 1.72-2.11 were also significantly lower than those of tracheophytes. The researchers interpreted these differences as adaptations to shade in the bryophytes, as well as the lower physiological activity of the bryophytes. The phaeopigments had a positive correlation with the chlorophyll content, a result of the presence of functional phaeophytin *a* in photosystem II. Chlorophyll degradation in the emersed bryophytes did not produce phaeopigments. Furthermore, the phaeopigment ratios had little variation with season or habitat. Summer desiccation was the primary factor related to pigment cycles, with strong chlorophyll content decreases in summer, accompanied by a decrease in the Chl *a*/*b* ratio. When bryophytes were continuously wet, the seasonal cycle was more attenuated and correlated more with changes in light conditions caused mostly by changes in canopy coverage. If the bryophytes were permanently immersed in sun-exposed habitats, both chlorophyll content and chlorophyll *a*/*b* ratio were high in all seasons, suggesting high metabolic activity all year. The leaf specific area and leaf specific weight were both comparable to those of terrestrial bryophytes and served to indicate the proportion of non-photosynthetic tissues and were related to desiccation and light tolerance of the species.

Seasons

Seasonal light differences can cause a shift in dominance of the stream macrophyte flora. Everitt and Burkholder (1991) suggested that the dominance of the red alga *Lemanea* (Figure 73) during cool months was due to its greater tolerance of high light intensities. When leaves returned to the trees, ***Fontinalis*** (Figure 5, Figure 6, Figure 12, Figure 20) species were able to dominate in the warmer months.

In the Riu Tenes, Catalonia, chlorophyll *a* increases in submerged mosses from December (after a dry period) to May (after a rainy period) (Peñuelas & Vallcorba 1988). On the other hand, the carotene:chl *a* ratio and phaeopigments increase following emergence. Thus, seasonal changes in pigment concentrations respond to microclimatic changes resulting from changes in the river level.

Martínez-Abaigar *et al*. (1994) analyzed seasonal changes in the photosynthetic pigments of 13 aquatic bryophytes. As in the study by López and Carballeira (1989), they found that chlorophyll contents (2.2-9.2 mg g^{-1} dry weight and 97-351 mg m^{-2} shoot area) were higher than those of terrestrial bryophytes, but were similar to those of epilithic river algae. They furthermore had a lower chlorophyll *a*:*b* ratio (2.1-2.8) and carotenoid index. In both bryophytes and algae, these are considered adaptations to shade conditions. They found that when chlorophyll degraded in the emersed bryophytes, no phaeopigments were produced. Furthermore, phaeopigments showed little variation with season or habitat. Seasonal differences were manifest as reduced chlorophyll in response to summer desiccation. This also caused a reduced chlorophyll *a*:*b* ratio, accompanied by an increase in the carotenoid:chlorophyll ratio. The seasonal cycles were less obvious in wet bryophytes, responding to changes in light conditions caused by leaf-out and leaf fall. For permanently submersed species, the chlorophyll content and chlorophyll *a*:*b* ratio were high in all seasons, indicating that these plants had a high metabolic state year-round.

Figure 73. ***Lemanea fluviatilis***, a red alga that thrives in streams in the cool months. Photo by J. C. Schou, with permission.

Martínez-Abaigar and Núñez-Olivera (2011) found that the moss ***Fontinalis antipyretica*** (Figure 12) showed some damage from enhanced UV radiation, mostly as brown coloration, development of the central fibrillar body in the cells, chloroplast disappearance, and protoplasts that became vesiculose to vacuolized to hyaline (Martínez-Abaigar *et al*. 2004b), but they noted that these symptoms are common as signals of stress from other causes. The one specific response demonstrated was a change in cell wall color from yellow to orange-brown (Martínez-Abaigar & Núñez-Olivera 2011)

Pigment concentrations track the opening and closing of the canopy (Álvaro 2001). Concentrations of nutrients tend to be lowest in spring and highest in autumn. This is due to dilution from the greater flow in spring and can relate to growth cycles and low flow in autumn. Although the light changes, the temperature variation in streams is much less than in the terrestrial environment.

UV-B

UV-B radiation is increasing as a result of ozone depletion in the upper atmosphere. The lack of a thick cuticle or epidermis, and often absence of multiple cell layers, suggests that bryophytes should be particularly susceptible to damage from this increased radiation. In the

aquatic environment, water can protect many species due to its ability to rapidly absorb the UV-B radiation and the canopy cover that diffuses much of it during the summer. But in mountain streams, the water may be insufficient to provide protection in this more exposed habitat. Furthermore, at low temperatures, ***Fontinalis antipyretica*** (Figure 12) suffers greater UV damage, but the aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) does not seem to respond differentially to temperature under UV stress (Núñez-Olivera *et al*. 2004). There also seems to be a direct relationship between UV tolerance and desiccation tolerance (Martínez-Abaigar & Núñez-Olivera 2011). This seems to be particularly true for ***Fontinalis antipyretica*** as it is among the most sensitive to both.

Figure 74. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, an aquatic species that seems to be indifferent to temperature under UV stress. Photo by Jan-Peter Frahm, with permission.

Some early studies recognized that UV light could damage sporelings. Kinugawa (1966) explored the damage and dark recovery in sporelings of ***Bryum pseudotriquetrum*** (Figure 72). Arróniz-Crespo *et al*. (2008b) found age-specific physiological responses to UV radiation in ***Jungermannia exsertifolia*** subsp. ***cordifolia***, an aquatic leafy liverwort. In the presence of enhanced UV radiation, some coumarin compounds only accumulated in older tissues (C3), whereas others were only in younger tissues (C4). The newly grown shoots showed the highest concentrations of chlorophylls, carotenoids, MEUVACs, and C4 in response to elevated UV.

Rader and Belish (1997) transplanted ***Fontinalis neomexicana*** (Figure 75) in a 10-week field experiment in a mountain stream to determine the effects of higher UV-B radiation. They irradiated transplants from shaded and sun-exposed sites and found that those from the open site exhibited an "important reduction" in dry biomass. On the other hand, those from the shaded site showed no effect on biomass. But they failed to show any net growth, and all samples lost material in these natural settings.

By contrast, Núñez-Olivera *et al*. (2005) demonstrated that previous light acclimation influenced degree of damage by enhanced UV radiation, with shade samples showing more effect than sun samples. This apparent protection of sun-adapted plants was evident in the sensitive ***Fontinalis antipyretica*** (Figure 12), but not in the UV-tolerant ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74). As further evidence of acclimation, Martínez-Abaigar *et al*. (2009) collected the same species from high altitudes and lower altitudes, finding that those from high altitudes (with greater UV radiation) were more tolerant of UV radiation.

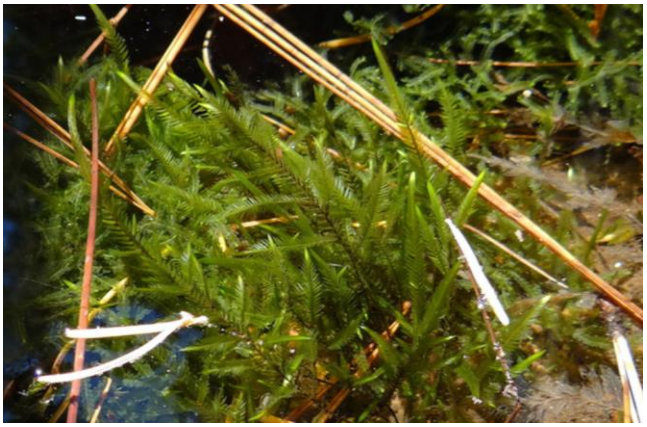

Figure 75. ***Fontinalis neomexicana***, a species in which sun-adapted populations can have a reduction in biomass accumulation when transplanted to the shade. Photo by Belinda Lo, through Creative Commons.

Martínez-Abaigar *et al*. (2003) considered the responses of ***Fontinalis antipyretica*** (Figure 12) and the leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) to elevated ultraviolet-B radiation. The responses were different between these two species. There was little response to UV-A radiation. With increased UV-B, ***Fontinalis antipyretica*** exhibited decreased chlorophyll and carotenoid concentration, chlorophyll *a*:*b* ratio, chlorophyll:phaeopigment ratio, net photosynthetic rate, light saturation point, maximum quantum yield of PS II, and apparent electron transport rate. Dark respiration increased, as did the **sclerophylly index** (ratio between dry mass and surface area of bryophyte shoot; see Montefort *et al*. 2018). But ***Jungermannia exsertifolia*** subsp. ***cordifolia*** showed only a reduction in **Fv/Fm** (measurement ratio that represents maximum potential quantum efficiency of Photosystem II if all capable reaction centers are open) and an increase in pigmentation. The production of UV-B-absorbing compounds (pigments) had rarely been reported in bryophytes when Martínez-Abaigar *et al*. (2003) conducted this study, particularly aquatic ones. Based on these response differences, the researchers warned against treating all bryophytes as one functional group, as has often been done in ecology.

In their study of bryophytes in mountain streams, Arróniz-Crespo *et al*. (2004) found differences among the species. They furthermore differed between 9 of the 10 mosses and the 4 liverworts in this study. Liverworts presented high levels of methanol-extractable UV-absorbing compounds, whereas these were low in all mosses except for ***Polytrichum commune*** (Figure 64-Figure 65). As noted by Crespo (2006), possible defense mechanisms have been characterized as both **constitutive** (always present) and **induced** (made present in response to a stimulus), differing greatly between mosses and liverworts.

Sun and Shade Plants

Núñez-Olivera and coworkers (Núñez-Olivera *et al*. 2005; Arróniz-Crespo *et al*. 2005) studied responses of the moss ***Fontinalis antipyretica*** (Figure 12) and the leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) to elevated UV-B, this time using sun- and shade-acclimated samples of each. Both sun and shade samples of ***Fontinalis antipyretica*** proved to be more sensitive than the liverwort following 78 hours of acclimation at 2ºC. Responses were similar to those of longer exposures (36-82 days). Shade samples were more sensitive only in ***Fontinalis antipyretica***, indicating some degree of acclimation in that species. For this species, Fv/Fm decreased 42% in the shade samples and only 27% in the sun samples at the end of the culture period. Neither sun nor shade samples of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** demonstrated significant differences between controls and UV-B-treated samples.

Soriano *et al*. (2019) assessed sun and shade adaptations and acclimation of stream bryophytes. These included ***Marchantia polymorpha*** subsp. ***polymorpha*** (Figure 55), ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74), and ***Fontinalis antipyretica*** (Figure 12). Of these, the two liverworts were more responsive to the radiation than the moss ***F. antipyretica***. Compared to shade plants of ***M. polymorpha***, they noted many changes in sun plants:

- higher **sclerophylly** (condition of thicker or firmer leaves, *i.e.* thallus)
- lower Chl *a* + *b* contents
- higher Chl *a*/*b* ratios
- higher ratios of (antheraxanthin + zeaxanthin): (violaxathin+ antheraxanthin + zeaxanthin)
- lower Fv/Fm values
- higher contents of methanol-soluble vacuolar UV-absorbing compounds (soluble UVACs)
- higher values of ratio between contents of methanol-insoluble cell wall-bound UVACs and soluble UVACs
- higher contents of insoluble *p*-coumaric and ferulic acids.

These responses reduced the light absorption, alleviated overexcitation, increased photoprotection by non-photochemical energy dissipation, provided UV screening and antioxidant capacity that increased UV protection, and resulted in photoinhibition. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** exhibited moderate differences between sun and shade populations, whereas those in ***F. antipyretica*** were indistinct. The response of the **xanthophyll index** (antheraxanthin + zeaxanthin):(violaxathin + antheraxanthin + zeaxanthin) was the most consistent response.

Photoprotective Pigments

Several researchers have reported photoprotective pigmentation in aquatic bryophytes grown in high light situations. Glime (1984) discovered red ***Fontinalis antipyretica*** (Figure 12) growing in cold water in full sunlight. These same leaves also had less chlorophyll than those grown in the shade. They exhibited greater specific leaf weight and less specific leaf area than the typical shade leaves. Nevertheless, there was no significant difference in the chlorophyll *a*:*b* ratio between the sun-acclimated and shade leaves.

López and Carballeira (1989) compared five species of aquatic bryophytes [***Fontinalis antipyretica*** (Figure 12), ***Brachythecium rivulare*** (Figure 66), ***Fissidens polyphyllus*** (Figure 67), ***Platyhypnidium riparioides*** (Figure 10), and the leafy liverwort ***Scapania undulata*** (Figure 8)] and their responses to stresses. The five species had higher chlorophyll concentrations than "some" terrestrial bryophytes. The stresses of organic and metal pollution were effective at changing the pigment ratios. They found that ***F. antipyretica*** was the most resistant species; ***S. undulata*** was the most sensitive. But what effects do these pigment changes have on the ability of these bryophytes to tolerate UV-B radiation and even high intensity PAR?

Martínez-Abaigar and Olivera (2007) noted that climate change and increasing UV-B could affect stream bryophytes. ***Fontinalis antipyretica*** (Figure 12) is sensitive and may be more sensitive when receiving enhanced UV-B at low temperatures. Shade plants of this species are more sensitive than sun plants. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) is relatively UV-B tolerant. Two of the five UV-B absorbing compounds in this species increase with altitude from 110-1800 m asl. At 2000 m asl these liverworts have a high UV-B absorption, whereas the ***F. antipyretica*** has low absorbance. When Martínez-Abaigar *et al*. (2003) compared a liverwort and a moss, the leafy liverwort ***Jungermannia exsertifolia*** experienced only a decrease in Fv/Fm, suggesting that this ratio and the concentration of UV-absorbing compounds were the most responsive indicators. These two responses can explain the greater tolerance of ***J. exsertifolia*** to enhanced UV light. The liverworts such as ***Jungermannia exsertifolia*** subsp. ***cordifolia*** appear to have higher concentrations of both constitutive and inducible methanol-extractable UV-absorbing compounds than do mosses (Martínez-Abaigar & Núñez-Olivera 2011).

Martínez-Abaigar and coworkers (Martínez-Abaigar *et al*. 2004a, 2006; Martínez-Abaigar & Núñez-Olivera 2011) found that in mountain streams the effects of UV-B exposure depended on the bryophyte species, environmental factors such as temperature, and location (sun or shade, low or high altitude). The liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) was a good bio-indicator of the light conditions. Variables such as Fv/Fm, concentrations of individual UV-absorbing compounds, and DNA damage were indicative of UV-B growing conditions. The most consistent indicators of damage by UV-B seem to be decreases in Fv/Fm, chlorophyll:phaeophyton, and of lesser importance decreases in chl *a*/*b* and net photosynthesis (Martínez-Abaigar & Núñez-Olivera 2011).

There is a natural gradient of increasing UV-B radiation as one ascends to higher altitudes. Arróniz-Crespo *et al*. (2006) explored this natural relationship at

elevations ranging from 1140 to 1816 m altitude. In ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74), they found two new caffeic acid derivatives: 5"(7"8"dihydroxycoumaroyl)-2-caffeoylmalic acid & 5"'-(7"8"dihydroxy-7-O-beta-glucosyl-coumaroyl)-2-caffeoyl-malic acid. In addition, they found phaselic acid (both in cis- & trans- forms) and feruloylmalic acid. These showed a significant linear relationship with altitude. The two new compounds, maximal apparent electron transport rate through PS II, and maximal non-photochemical quenching all increased with altitude. At the same time, the photoinhibition percentage decreased. The researchers suggested that this increase in some of these secondary compounds may permit the tolerance of this liverwort to the UV-B irradiance at high elevations.

Arróniz-Crespo *et al*. (2008a) further explored the possible substances that provided protection from enhanced UV radiation. After exposure to enhanced UV radiation for 82 days, they examined five hydroxycinnamic acid derivatives. They reasoned that in its high mountain habitat with high UV radiation and low temperatures, it must have something to protect it. In particular, it showed little damage to the Fv/Fm ratio or chlorophyll:phaeopigment ratio in response to elevated UV radiation. They attributed this stability to the presence of three hydroxycinnamic acid derivatives: p-coumaroylmalic acid, 5"-(7",8"-dihydroxycoumaroyl)-2-caffeoylmalic acid, and 5"-(7",8"-dihydroxy-7-O-ß-glucosyl-coumaroyl)-2-caffeoylmalic acid. These are apparently induced in the liverwort by exposure to UV radiation.

In a laboratory experiment, Martínez-Abaigar *et al*. (2009) cultured three leafy liverworts [***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74), ***Marsupella sphacelata*** (Figure 76), ***Scapania undulata*** (Figure 8)] and three mosses [***Brachythecium rivulare*** (Figure 66), ***Bryum pseudotriquetrum*** (Figure 72), ***Racomitrium aciculare*** (Figure 77)] under enhanced UV-B radiation (10.3 kJ m^{-2}) as would be expected with a 20% ozone depletion. After 20 days of culture, they found that the culture conditions had a greater influence than did the enhanced UV radiation. Responses to both factors depended on the species and the variable considered. Both photosynthetic pigments and photosynthetic performance were negatively affected by the culture conditions, but only in ***Marsupella sphacelata*** was growth impeded. Enhanced UV-B, on the other hand, did not affect photosynthetic performance, but did affect growth in ***Jungermannia exsertifolia*** subsp. ***cordifolia***. There was rarely any increase in UV-protective compounds under this level of UV-B. These species had been collected at high altitudes (1850-2000 m asl) and were most likely already acclimated to high UV-B levels. This study supports previous studies in indicating that the location and collection date are important in acclimation to UV-B.

Otero *et al*. (2009) analyzed 135 herbarium samples of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) from northern Europe for UV absorbance in methanolic extracts. They also analyzed five specific hydroxycinnamic acid derivatives – UV-absorbing compounds. This demonstrated that the UV absorbance and compound levels showed a positive correlation with year during the sampling period of 1850-2006. *p*-coumaroylmalic acid (C1) was the only compound showing a significant (and negative) correlation with the stratospheric ozone and UV irradiance for the period of available data. Most specimens were from July-August, but the highest stratospheric ozone occurred in June. Nevertheless, there was no long-term temporal trend. UV values were higher in June-July than in August. In short, levels of *p*-coumarolymalic acid did not suggest any significant temporal trend during the study periods for which data were available.

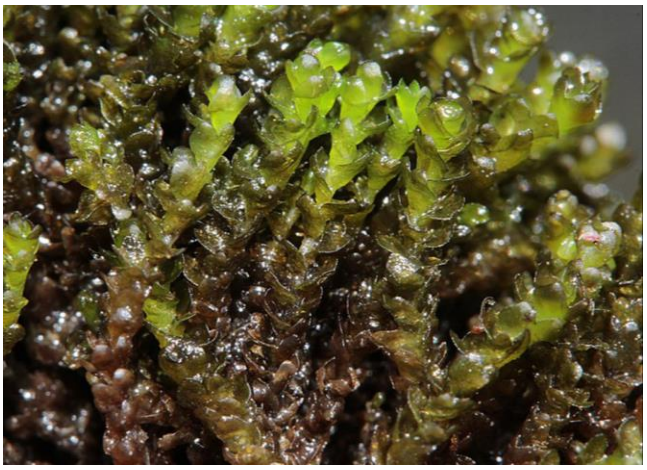

Figure 76. ***Marsupella sphacelata***, a species for which growth was impeded by enhanced UV-B radiation. Photo by Hermann Schachner, through Creative Commons.

Figure 77. ***Racomitrium aciculare***, a species that responded more to culture conditions than to UV-B radiation enhancement. Photo by Hugues Tinguy, with permission.

In the Tierra del Fuego of Argentina, the high elevation means that UV-B is higher than in other aquatic habitats. After analyzing five liverworts and ten mosses from unshaded aquatic bryophytes, Otero *et al*. (2008) concluded, as had others mentioned here, that species

differed. Spectral peaks ranged from none to 2 defined peaks, probably due to phenolic derivatives that could serve as both screening compounds and antioxidants. The absorbance curves of most liverworts were higher than those of most mosses. The liverworts ***Noteroclada confluens*** (Figure 78) and ***Triandrophyllum subtrifidum*** (Figure 79), in particular, showed higher bulk UV-absorption capacity in methanolic extracts. They concluded that while the accumulation of UV-absorbing compounds commonly protects liverworts against UV radiation, that rarely occurs in mosses.

Figure 78. ***Noteroclada confluens*** with antheridia, a species with higher UV-absorption capacity than that found in mosses. Photo by Li Zhang, with permission.

Figure 79. ***Triandrophyllum subtrifidum***, a species with higher UV-absorption capacity than that found in mosses. Photo by Shirley Kerr, with permission.

Cell Wall vs Soluble Compounds

Fabón *et al*. (2010) examined the cell compartments where hydroxycinnamic acid derivatives reside in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) as a response to elevated UV-B. The bulk UV absorbance of the soluble fraction was higher than that of the cell-wall-bound fraction. Absorbances by both fractions increased under elevated UV-B. Five different hydroxycinnamic acid derivatives were located in the soluble fraction, with two additional ones in the cell-wall-bound fraction, but only p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell-wall-bound fraction increased in response to elevated UV-B. Both maximum quantum yield of PS II and DNA were damaged more strongly when the UV-B was elevated. The researchers concluded that the soluble and cell-wall-bound fractions responded differently as protective mechanisms.

Fabón *et al*. (2012) found that **diel** (within 24 hours) differences existed in both the soluble and cell-wall fractions of UV-absorbing compounds in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74). They were able to respond within a few hours to radiation changes. Furthermore, components of the xanthophyll cycle made rapid and significant diel changes in response to high PAR, UV-A, and UV-B radiation. This causes dynamic photoinhibition responses and protection of PS II.

Soriano *et al*. (2019) concluded that the responses of aquatic bryophytes were influenced by both the **PAR** (photosynthetically active radiation) and UV radiation. They found that soluble UV-absorbing compounds (UVACs) generally had clearer responses than did the insoluble UVACs. They attributed this to the fact that insoluble UVACs are relatively immobilized in the cell wall. Under conditions close to ambient, sclerophylly and Chl *a* + *b* content were influenced only by PAR and Fv/Fm. Luteolin and apigenin derivatives were determined by UV. The xanthophyll index was influenced by both types of radiation.

Montefort *et al*. (2018) found that mosses had lower levels of mainly vacuolar soluble UV-absorbing compounds (UVACs) but higher cell-wall-bound insoluble UVACs when compared to liverworts. This suggests that mosses should have greater tolerance of UV radiations, explaining their greater frequency in areas with high levels of UV radiation. Nevertheless, the relationships between UVACs and the ecological parameters they considered were weak. From this they concluded that UVACs might be primarily constitutive in bryophytes, *i.e.* depending on phylogeny more than on habitat. Nevertheless, water restrictions and high sun exposures increased sclerophylly, suggesting a physiological response.

UV Interactions

Martínez-Abaigar and Núñez-Olivera (2011) suggested that we might expect increased UV damage when heavy metals add to the stress. They were able to demonstrate this with cadmium and UV radiation in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74), with both causing loss of chlorophyll, strong inhibition of PS II, and an increase in the xanthophyll index, with greater effects under combined treatment. Cadmium affected the photosynthetic rate, but enhanced UV radiation did not. Both treatments increased the concentrations of UV-absorbing compounds.

When UV stress is combined with other stress factors, it becomes even a greater stressing agent. After 15 days of cultivation of the aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74), Otero *et al*.

(2006) found that both cadmium and enhanced UV radiation caused the degradation of chlorophyll and a decrease in the maximum quantum yield of PS II, while resulting in an increase in the mechanisms of non-photochemical dissipation of energy (increase in the xanthophyll index). Cadmium proved to be more stressing than did enhanced UV radiation. The increased UV radiation caused the level of trans-*p*-courmaroylmalic acid to increase, whereas cadmium caused an increase in trans-phaselic and feruloylmalic acids. Furthermore, UV-B radiation caused DNA damage, but this was intensified in the presence of cadmium. Cadmium and other metals impair the DNA enzymatic repair mechanisms.

Photoinhibition

Maberly (1985) found no evidence of photoinhibition at 7 levels of photon irradiance and 5-6 CO_2 concentrations in ***Fontinalis antipyretica*** (Figure 12) during four months at ambient temperature. The light compensation point for these populations was generally lower than most published values. He noted the importance of the interaction between light intensity, CO_2 concentration, and temperature on the levels of net photosynthesis. Effects of increased light levels is dependent on availability of CO_2 and loss of carbon through photorespiration as the temperature rises.

On the other hand, Rader and Belish (1997) concluded that photoinhibition increases under 15-40% UV-B increase and may be harmful to aquatic mosses such as ***Fontinalis neomexicana*** (Figure 75). This species had no effects by increased UV-B in the shade (biomass 28.47 mg cm^{-2}), but in the open it produced lower biomass (19.57 mg cm^{-2}). Subsequently, Soriano *et al*. (2019) similarly indicated that photoinhibition can occur in aquatic bryophytes.

It appears that photoinhibition can even affect nitrification in streams, as noted in bryophyte enclosures of non-acidified streams in the alpine zone of the High Tatra Mountains along the border of northern Slovakia in the Prešov Region and southern Poland in the Lesser Poland Voivodeship (Kopacek & Blazka 1994).

Effects of Nutritional Status

The ability of plants to make various compounds depends on their nutritional status. Martínez-Abaigar *et al*. (2008) improved the phosphorus availability to the liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 74) and the moss ***Fontinalis antipyretica*** (Figure 12) to determine effects on several UV responses in lab experiments. After 36 days there were no differences between bryophytes in the P-enhanced and normal P conditions for any of the measured UV response factors, except for the vitality index OD430/OD410 in ***J. exsertifolia***. These bryophytes have low nutritional requirements, so it is likely that the additional P was not needed, particularly in the absence of any other nutrient additions.

Although the addition of phosphorus, typically a limiting nutrient in streams, helps to protect some microalgae, this has not been observed in aquatic bryophytes (Martínez-Abaigar & Núñez-Olivera 2011). In two bryophytes from mountain streams, an increase of P 1.7- to 3.7-fold did not alter the responses to enhanced UV radiation (Martínez-Abaigar *et al*. 2008). It might be instructive to test the same enhancement of P on lower elevation aquatic bryophytes that did not have any natural acclimation to UV radiation.

Temperature

Our field experience tells us that temperature can be a limiting factor for bryophytes, including those in streams. Ewart (1895-1897) contended that the ability to withstand temperature extremes is directly related to the moisture content of the plants. But studies that examine other effects on photosynthesis and growth in bryophytes are rare.

We have seen in subchapter 2-4 of this volume that temperature governs periods of growth and rhizoid production in species of ***Fontinalis***. Maberly (1985) noted that the slope of photosynthesis vs CO_2 concentration increased linearly as temperature increased, an observation that is consistent with the effects of boundary-layer resistance.

High Temperatures

Bryophytes in the water seem to be particularly susceptible to high temperatures. They are hydrated and thus are able to respire. But they are C_3 plants and as the temperature goes up, so does the photosynthetic product, but also so does the respiratory rate, only faster. Irmscher (1912) cultured many mosses at various temperatures and found that ***Fontinalis antipyretica*** (Figure 12) and ***F. squamosa*** (Figure 1) were still alive at 20ºC, but at 30ºC ***F. antipyretica*** was dead. ***Drepanocladus aduncus*** (Figure 19), a species that occurs in shallow water of lakes, pools, ditches, and fens, did not fare any better at these two temperatures. But the ***Fontinalis*** did not fare well at -15ºC, with both species dying in both submersed and turgescent conditions; at -10ºC, ***F. antipyretica*** survived.

My experience in the tropics is limited, but in the lowland forest streams there we would expect the combination of low light and high temperatures to cause respiration to exceed photosynthesis (Vitt & Glime 1984; Glime & Gradstein 2018). On the other hand, in higher elevations in the tropics, temperatures remain cool enough for a number of species to survive.

Carballeira *et al*. (1998) subjected ***Fontinalis antipyretica*** (Figure 12) to temperatures ranging 16ºC-34ºC. They found responses (pigment ratio, photosynthetic and respiratory rates) did not differ between mosses collected from a "normal" river and one subjected to abnormally high temperatures resulting from hotspring waters. They also subjected mosses to 30ºC for 2, 4, and 10 days, then transferred them to 16ºC for 40 days. Even those held at 30ºC for 10 days exhibited good recovery.

Nevertheless, Ceschin *et al*. (2012) found that few aquatic bryophyte species prefer higher temperatures.

Hygroamblystegium fluviatile (Figure 80) and ***Leptodictyum riparium*** (Figure 69) exhibited temperature optima of 18ºC and above. Other species exhibited temperature preferences below 12ºC, including ***Palustriella commutata*** var. ***commutata*** (Figure 37), ***Cratoneuron filicinum*** (Figure 41), ***Fissidens viridulus*** (Figure 81), and ***Cinclidotus aquaticus*** (Figure 34).

Figure 80. ***Hygroamblystegium fluviatile***, a species with a high temperature optimum (18ºC) compared to other aquatic mosses. Photo by Michael Lüth, with permission.

Figure 81. ***Fissidens viridulus***, a species that prefers temperatures below 12ºC. Photo by Jan-Peter Frahm, with permission.

Sanford (1979) found that ***Leptodictyum riparium*** (Figure 69) exhibited branch proliferation under high temperature stress. This ability to produce new branches decreased later in the experiments. The apices of branches and the main axis seemed to be the most heat-resistant parts of this species. Glime and Carr (1974) found a similar resistance in the apices of ***Fontinalis*** in New Hampshire, USA (Figure 82). They were able to demonstrate this in ***Fontinalis*** species that were boiled for 12 hours per day for two weeks. The mosses were returned to their native stream and one stem produced a green leaf within the next year. All other leaves were dead or gone.

Sanford *et al*. (1974) observed growth of ***Hygrohypnum ochraceum*** (Figure 23) in relation to temperature in the Sacramento River. When temperatures were above 26ºC, some of the stem tips died. After four weeks at 30ºC all plants died. The temperature optimum for growth ranged ~17-21ºC. Sanford (1979) found that ***Leptodictyum riparium*** (Figure 69) had its optimum growth at 23ºC, with death occurring at 33ºC.

Figure 82. Labelled rocks with ***Fontinalis*** spp. from the Glime and Carr 1974 temperature experiment. Photo by Janice Glime.

Not surprisingly, species differ in their response to temperature. Arscott *et al*. (2000) found that ***Schistidium agassizii*** (Figure 21) could persist in the Kuparuk River, Alaska, with cold, low-nutrient conditions, but ***Hygrohypnum alpestre*** (Figure 22) and ***H. ochraceum*** (Figure 23) could not. In fact, the ***Hygrohypnum*** species were able to take advantage of the elevated light and temperatures (>20ºC) with greater net primary production. On the other hand, these two species were more affected by desiccation than was ***S. agassizii***.

Bryophytes are C_3 plants. This means that they have a low temperature compensation point and high levels of photorespiration as the temperature increases. Carballeira *et al*. (1998) found that ***Fontinalis antipyretica*** (Figure 12) did not exhibit any difference in physiological response to temperature between populations from a normal river and one with abnormally high temperatures. In fact, after exposure to temperatures of 30ºC for up to 10 days, these mosses showed good recovery after 40 days at 16ºC.

Elevated temperatures can change the absorption rate for substances in the water. Martins *et al.* (2004) found that some metal elements increase in their absorption, but others do not. For example, maximum biosorption capacity for cadmium by ***Fontinalis antipyretica*** (Figure 12) did not change with elevated temperatures, but for zinc the capacity increased with temperature from 11.5 mg g^{-1} at 5ºC to 14.7 mg g^{-1} at 30ºC.

Bryophytes are able to acclimate to temperatures through heat hardening. Temperatures above the optimum can increase their thermal resistance, as has been noted in flowering plants (Antropova 1974). For example, the wetland emergent ***Sarmentypnum sarmentosum*** (Figure 83) shifts its optimum temperature from 19ºC in July to 11ºC in August to 16ºC in September (Oechel 1976). This change seems to correspond to moisture availability. Vitt and Pakarinen (1977) likewise found moisture to be of major importance to emergent mosses in the High Arctic.

Figure 83. ***Sarmentypnum sarmentosum***, a wetland species that has seasonal changes in its optimum temperature. Photo by David T. Holyoak, with permission.

Low Temperatures

Limiting factors in streams are different from those on land and even some in lakes and ponds. And winter temperatures in temperate and arctic streams can be more severe while open water remains in a partially frozen stream. Our data from New Hampshire streams indicated the temperature of flowing water in one such partially frozen stream remained at 0.8-1.0ºC throughout the winter.

Temperature is an important stimulant in the production of pigments (Martínez-Abaigar & Núñez-Olivera 2018). Cold temperatures can cause the formation of red pigments, particularly in high light, as discussed above (Glime 1984). Presumably this protects the chlorophyll from high excitation when the temperature slows the physiological protections against photodamage.

Cold temperatures are not usually a problem in streams because the streams typically do not freeze to the bottom. And even if the mosses are frozen in ice, the ice and snow on top of the ice insulate them from lower temperatures. Growth can even occur at low temperatures. Sanford *et al*. (1974) found that in the Sacramento River, ***Hygrohypnum ochraceum*** (Figure 23) experienced growth at temperatures as low as 4ºC.

Dilks and Proctor (1975) also demonstrated the ability of the bryophytes to withstand sudden cold temperatures. Most of the tested species survived rapid cooling to -5ºC for 6 hours. They seem to be protected from intracellular freezing under normal cooling processes by withdrawal of water, most likely by extracellular ice crystals, much like events causing freezer burn in a deep freeze. But in the case of the bryophytes, this withdrawal prevents formation of ice crystals within the cells, thus preventing damage to the cell membranes and organelles. When temperatures warm, the water again enters the cells of the bryophytes and they return to normal activity unharmed. This is more easily accomplished when all leaf cells contact the atmosphere than in the multi-layered leaves of tracheophytes. On the other hand, the stream bank bryophytes ***Conocephalum conicum*** (Figure 35) and ***Pellia epiphylla*** (Figure 71) were killed by rapid cooling to -5ºC.

Fissidens fontanus (Figure 84) was killed when frozen in ice at -5ºC, but was able to maintain luxurious growth where it lived on rocks exposed to sub-zero temperatures above water (Lohammar 1954). Lohammar suggested that the basal portion was more resistant, thus permitting the above-water plants to survive. ***Fissidens crassipes*** (Figure 85) spread when the temperature of the Rhine was elevated 2ºC by industrial waste, eliminating most of the ice drift and revealing another cause of winter loss – destruction by ice flow (Florschütz *et al*. 1972).

Freezing can kill emergent mosses such as ***Drepanocladus*** cf. ***aduncus*** (Figure 19) and ***Sarmentypnum sarmentosum*** (Figure 83) (Priddle 1979). But they did survive in an Antarctic lake that did not freeze where they were growing. On the other hand, ***Fontinalis antipyretica*** (Figure 12) and ***Drepanocladus aduncus*** survived to -10ºC, whereas when turgescent these mosses died at that temperature, as did most of the terrestrial bryophyte species.

Figure 84. ***Fissidens fontanus***, a species that died at -5ºC in ice but survived and grew at even lower temperatures in air. Photo by Walter Lampa, through Creative Commons.

Figure 85. ***Fissidens crassipes*** with capsules, a species that spread when the temperature rose by 2ºC in the Rhine. Photo by Michael Lüth, with permission.

Optimum Temperatures

Dilks and Proctor (1975) used manometry to compare assimilation of bryophytes, including the aquatic species ***Fontinalis squamosa*** (Figure 1) and ***Nardia compressa*** (Figure 86), at various temperatures. In these experiments, the carbon dioxide concentrations were high, permitting the optimum temperature for net assimilation to occur at ~25-30ºC. The temperature compensation point occurred at ~35-40ºC. Unlike most of the terrestrial bryophytes, the aquatic moss ***Fontinalis squamosa*** had its optimum oxygen production (measure of photosynthesis) at 15-20ºC. The aquatic leafy liverwort ***Nardia compressa*** had its maximum photosynthesis at 20ºC.

Figure 86. ***Nardia compressa***, a leafy liverwort that can have its maximum photosynthesis at 20ºC. Photo by Hermann Schachner, through Creative Commons.

Other similar temperature optima have been reported in aquatic species. Zastrow (1934) found the optimum for wetland species in his study to be 15-20ºC. Saitoh *et al*. (1970) similarly found 20ºC to be the optimum for ***Fontinalis hypnoides*** (Figure 87). But the Keweenaw Peninsula, Michigan, populations of six species of ***Fontinalis*** indicated that these species could not sustain growth at temperatures above 15ºC for a long time. In fact, some [***F. neomexicana*** (Figure 75) and ***F. dalecarlica*** (Figure 5)] had maximum growth at 10ºC (Glime & Acton 1979; Glime 1982). The wetland species ***Sarmentypnum sarmentosum*** (Figure 83) can spend 10 months of the year experiencing temperatures above its low temperature compensation point due primarily to a very low respiration rate at low temperatures (Priddle 1982). On the other hand, the aquatic ***Racomitrium aquaticum*** (Figure 45) requires 64 days at 37ºC to experience 50% chlorophyll loss. At 20º it requires 200 days, whereas in the terrestrial ***R. lanuginosum*** (Figure 46) it requires 400 days.

Using manometry, Glime and Acton (1979) cultured ***Fontinalis duriaei*** (Figure 88) from Houghton County, Michigan, USA, with its associated periphyton at five temperatures from 1 to 20ºC and at 3 light levels (2400, 5400, 10,800 lux). At the mid light level, this population experienced its peak assimilation at 10ºC, a combination that would typically occur in its native stream shortly after snow melt and again in the autumn, the two periods when this population experiences its greatest growth in nature. The level of 5400 lux was indicated as the level of **light saturation** (light level where increasing the light does not increase photosynthetic rate) under the CO_2 conditions of the experiments. Further experiments are needed in which CO_2 gas is bubbled into the containers during measurement to avoid depletion.

Figure 87. ***Fontinalis hypnoides***, a species that can reach an optimum at temperatures as high as 20ºC. Photo by Jean Faubert, with permission.

Fontinalis antipyretica (Figure 12) and ***Leptodictyum riparium*** (Figure 69) in culture showed contrasting growth optima of 10ºC and 23ºC, respectively (Glime 1982), but in the study by Vanderpoorten *et al*. (1999) both species had similar broad ranges. In separate studies, Glime and Acton (1979) and Fornwall and Glime (1982) demonstrated acclimation to the temperature in species of ***Fontinalis***, as well as geographic differences, which could account for the differences observed by Vanderpoorten and coworkers.

Figure 88. ***Fontinalis duriaei***, a species that at 5400 lux experiences its peak assimilation at 10ºC. Photo by Michael Lüth, with permission.

Crombie and Paton (1958) found that temperature can affect seta elongation in liverworts. They found that if older sporophytes of the stream bank ***Pellia epiphylla*** (Figure 71) are left in the field until January or February, they will respond more rapidly to a temperature stimulus than those collected in early autumn. This could occur as a result of slow accumulation of growth hormones stimulated by temperature and/or light. Possible substances include IAA (Asprey *et al.* 1958), gibberellins (Brian & Hemming 1958), and 2,4-dichlorophenoxyacetic acid (Benson-Evans 1961).

While there are a number of experimental studies on the effects of temperature, the physiological responses outside photosynthesis and growth remain largely undocumented. My own experience suggests that at high temperatures the mosses lose color, suggesting chlorophyll damage. A secondary problem is that the higher temperatures can favor the growth of bacteria and algae, thus blocking light.

Bryophyte Antifreeze

Investigations on the fatty acid content of mosses indicate high levels of C_{22} acids, but low levels of C_{18} fatty acids that are typical of xerophytic mosses (Anderson *et al*. 1974). ***Fontinalis antipyretica*** (Figure 12) has the angiospermous type of fatty acids and the lowest concentration of algal fatty acids of any bryophyte tested (Karunen 1982). But the emergent ***Drepanocladus*** *s.l.* (Figure 19) was in the middle and ***Calliergon*** (Figure 51) had algal fatty acids. ***Fontinalis*** has the arachidonic acid prostaglandin (Asakawa, pers. comm.), a fatty acid known to be important in keeping footpads pliable in Arctic rodents (Prins 1981). Could these arachidonic acids help the aquatic bryophytes to survive at low temperatures?

Temperature Effects on Absorption

As we should expect, temperature affects absorption rate. But these effects on heavy metals are not all the same. In ***Fontinalis antipyretica*** (Figure 4), temperature had little or no effect on the absorption rate of cadmium, whereas zinc absorption increased with temperature from 11.5 mg g^{-1} moss at 5ºC to 14.7 mg g^{-1} moss at 30ºC (Martins *et al*. 2004). These temperature relationships will be discussed further in subchapter 2-7 of this volume.

Summary

Bryophyte lineages have been back and forth between land and water. This has provided them with a genetic background that gives rise to a variety of physiological adaptations. This is beneficial in permitting them to live where seasonal water level changes occur. Even the aquatic moss ***Fontinalis*** is able to survive in a dry stream for several months. When water returns, leaf and plant fragments can be dispersed and develop new plants. Stems, in particular, are highly resistant and can produce protonemata or rhizoids and branches.

When aquatic mosses are stranded out of water, they become pale, with less chlorophyll, but develop more chloroplasts. Chlorophyll *a* is damaged more than chlorophyll *b*. More chlorophyll is lost at higher temperatures. Damage to cellular membranes causes electrolyte leakage, especially potassium, as well as carbohydrates, amino acids, and other organic compounds. Some of these are reabsorbed upon rewetting. More sugar and less protein are produced during dehydration; the reverse is true during rehydration. Irreversible loss of polyribosomes occurs during dehydration. Amphibious species may develop denser tissues and more denticulations out of water. Heterophylly resulting from submersion vs emersion does not seem to occur in bryophytes, but experimentation is needed. Growth forms must balance light capture with water retention and drag reduction. Changes in allocation can result from changes in water availability.

Slow drying is important in survival; growth form can slow the rate. But amount of water lost seems to have the greatest effect on membrane integrity and photosynthesis. In a natural stream, where drying is usually slow, it can take 1-4 weeks to cause cellular damage. Emergent mosses take longer. There is a peak in photosynthesis during the initial phase of water loss. Photosynthetic efficiency is important in rate of recovery. The respiratory burst upon rewetting is shorter in wet-adapted species.

Truly aquatic species seem to have less desiccation tolerance, but laboratory studies must be viewed with caution because of the rapid rate of drying in most. Nevertheless, some aquatic species have pectic substances in the cell walls that permit rapid water intake, especially in the stems. Gibberellic acid, ethylene, and abscisic acid should be explored for their role in adaptations to immersion-emersion.

High light levels during emersion can stimulate production of colored pigments, especially red. Pigments in bryophytes are mostly the same as those in tracheophytes. Low light levels cause bryophytes to have more chlorophyll *b* and lower *a*:*b* ratios. Pigment concentrations change seasonally and track opening and closing of the canopy and periods of desiccation. Osmotic values seem to be correlated with light intensity, but not with moisture.

Increased UV-B causes a decrease in chlorophyll and carotenoid concentration, chlorophyll *a*:*b* ratio, chlorophyll:phaeopigment ratio, net photosynthetic rate, light saturation point, maximum quantum yield of PS II, and apparent electron transport rate, with an increase in protective pigmentation and a higher xanthophyll index. Defense mechanisms are both constitutive and induced. Acclimation occurs to some degree. Many liverworts seem to produce higher levels of methanol-extractable UV-absorbing compounds compared to most mosses. Hydroxycinnamic acid derivatives seem to be among the protective substances. Mosses tend to put more

protective compounds in the cell walls, whereas the liverworts put them within the cells.

Enhanced UV-B can affect growth without affecting photosynthetic performance. Photoinhibition can increase. Negative effects of UV can increase when coupled with heavy metals. Nutrient levels often do not affect the response to UV-B, perhaps because of the slow growth and low needs for nutrients.

Most aquatic bryophytes prefer cooler temperatures, but optimum temperatures range 10º-30ºC. Nevertheless, they have good recovery after short periods of temperatures of 30ºC. And they are able to acclimate their photosynthetic rate. Freezing can kill emergent mosses. Temperature affects absorption rates of different nutrients and heavy metals differently. Higher temperatures can cause chlorophyll damage and invasion of periphytic bacteria and algae that block light. Fatty acids, especially arachidonic acid, may keep membranes pliable and protect the bryophytes from membrane damage at cold temperatures.

When light levels are low and temperatures high, respiration exceeds photosynthesis. There is an interaction between light intensity, CO_2 concentration, and temperature on the rate of net photosynthesis.

Acknowledgments

Many Bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. Thank you to Josep Peñuelas for sending me the paper on the evolution of sclerophylly. Maria Arróniz-Crespo provided me with a needed paper. Javier Martínez-Abaigar has provided with many of the papers from his lab regarding UV-B radiation and pigmentation.

Literature Cited

Abel, W. O. 1956. Die Austrocknungresistenz der Laubmoose. Österr. Akad. Wiss. Math.-Naturwiss. Klasse, Sitzungsberichte, Abteilung 1 165: 619-707.

Álvaro, M. A. G. 2001. Contenido de nutrientes minerales y composición pigmentaria fotosintética en briófitos acuáticos: Una perspectiva ecofisiológica. [Content of mineral nutrients and photosynthetic pigment composition in aquatic bryophytes: An ecophysiological perspective.]. Rev. Ecosist. 10(1): 26-27.

Anderson, W. H., Hawkins, J. M., Gellerman, J. L., and Schlenk, H. 1974. Fatty acid composition as a criterion in taxonomy of mosses. J. Hattori Bot. Lab. 38: 99-103.

Antropova, T. A. 1974. Temperature adaptation studies on the cells of some bryophyte species. Tsitologiia 16: 38-42.

Arróniz-Crespo, M., Núñez-Olivera, E., Martínez-Abaigar, J., and Tomás, R. 2004. A survey of the distribution of UV-absorbing compounds in aquatic bryophytes from a mountain stream. Bryologist 107: 202-208.

Arróniz-Crespo, M., Núñez-Olivera, E., Martínez-Abaigar, J., Tomas, R., Beaucourt, N., and Otero, S. 2005. Effects of an altitude-dependent natural gradient of UV-B radiation on the physiology of sun and shade populations of an aquatic liverwort. Abstract. In: XVII International Botanical Congress, Vienna, Austria, Austria Center Vienna, 17-23 July 2005, Abstracts, p. 105.

Arróniz-Crespo, M., Núñez-Olivera, E., Martínez-Abaigar, J., Becker, H., Scher, J., Zapp, J., Tomás, R., and Beaucourt, N. 2006. Physiological changes and UV protection in the aquatic liverwort *Jungermannia exsertifolia* subsp. *cordifolia* along altitudinal gradient of UV-B radiation. Funct. Plant Biol. 33: 1025-1036.

Arróniz-Crespo, M., Núñez-Olivera, E., and Martínez-Abaigar, J. 2008a. Hydroxycinnamic acid derivatives in an aquatic liverwort as possible bioindicators of enhanced UV radiation. Environ. Pollut. 151: 8-16.

Arróniz-Crespo, M., Phoenix, G., Núñez-Olivera, E., and Martínez-Abaigar, J. 2008b. Age-specific physiological responses to UV radiation in the aquatic liverwort *Jungermannia exsertifolia* subsp. *cordifolia*. Cryptog. Bryol. 29: 115-126.

Arscott, D. B., Bowden, W. B., and Finlay, J. C. 2000. Effects of desiccation and temperature/irradiance on the metabolism of 2 Arctic stream bryophyte taxa. J. N. Amer. Benthol. Soc. 19: 263-273.

Asprey, G. F., Benson-Evans, K., and Lyon, A. G. 1958. Effect of gibberellin and indoleacetic acid on seta elongation in *Pellia epiphylla*. Nature 181: 1351-1351.

Bendz, G., Loöf, L. G., and Martensson, O. 1968. Moss pigments. 8. The carotenoids of *Fontinalis antipyretica* L. ex Hedw. Acta Chem. Scand. 22: 2215-2218.

Benson-Evans, K. 1961. Environmental factors and bryophytes. Nature (London) 191: 255-260.

Bewley, J. D. 1974. Protein synthesis and polyribosome stability upon desiccation of the aquatic moss *Hygrohypnum luridum*. Can. J. Bot. 52: 423-427.

Boston, H. L., Farmer, A. M., Madsen, J. D., Adams, M. S., and Hurley, J. P. 1991. Light-harvesting carotenoids in two deep-water bryophytes. Photosynthetica 25: 61-66.

Bowden, W. B., Finlay, J. C. and Maloney, P. E. 1994. Long-term effects of PO_4 fertilization on the distribution of bryophytes in an Arctic river. Freshwat. Biol. 32: 445-454.

Brian, P. W. and Hemming, H. G. 1958. Complementary action of gibberellic acid and auxins in pea internode extension. Ann. Bot. 22: 1-17.

Burr, G. O. 1941. Photosynthesis of algae and other aquatic plants. In: Needham, J. G. Symposium on Hydrobiology. Univ. Wisc. Press, Madison, pp. 163-181.

Carballeira, A., Díaz, S., Vázquez, M. D., and López, J. 1998. Inertia and resilience in the responses of the aquatic bryophyte *Fontinalis antipyretica* Hedw. to thermal stress. Arch. Environ. Contam. Toxicol. 34: 343-349.

Carvalho, R. C. de. 2009. Desiccation in the aquatic bryophyte *Fontinalis antipyretica*. XVII Simpósio Botânica Criptogâmica, 24 September 2009. <http://lisboa.academia.edu/RicardoCruzdeCarvalho/Talks/36958/Desiccation_in_the_aquatic_bryophyte_Fontinalis_antipyretica>.

Carvalho, R. C. de. 2013. Coping with extreme dehydration: A physiological, biochemical and molecular study on the aquatic bryophyte *Fontinalis antipyretica*. Tese de doutoramento, Biologia (Fisiologia e Bioquímica), Universidade de Lisboa, Faculdade de Ciências.

Carvalho, R. C. de, Branquinho, C., and Silva, J. M. da. 2011. Physiological consequences of desiccation in the aquatic bryophyte *Fontinalis antipyretica*. Planta 234: 195-205.

Carvalho, R. C. de, Catalá, M., Silva, J. M. da, Branquinho, C., and Barreno, E. 2012. The impact of dehydration rate on the production and cellular location of reactive oxygen species in an aquatic moss. Ann. Bot. 110: 1007-1016.

Carvalho, R. C. de, Silva, A. B. da, Soares, R., Almeida, A. M., Coelho, A. V., Silva, J. M. da, and Branquinho, C. 2014. Differential proteomics of dehydration and rehydration in bryophytes: evidence towards a common desiccation tolerance mechanism. Plant Cell Environ. 37: 1499-1515.

Carvalho, R. C. de, Silva, A., Branquinho, C., and Silva, J. 2015. Influence of dehydration rate on cell sucrose and water relations parameters in an inducible desiccation tolerant aquatic bryophyte. Environ. Exper. Bot. 120: 18-22.

Ceschin, S., Aleffi, M., Bisceglie, S., Savo, V., and Zuccarello, V. 2012. Aquatic bryophytes as ecological indicators of the water quality status in the Tiber River basin (Italy). Ecol. Indic. 14: 74-81.

Crespo, M. A. 2006. Efectos de la radiación ultraviolet-B sobre briófitos acuáticos de ríos de montaña. [Effects of ultraviolet-B radiation on aquatic bryophytes of mountain rivers.]. Bol. Soc. Españ. Briol. 28: 102-103.

Crombie, W. M. and Paton, J. A. 1958. Age effect on seta elongation in *Pellia epiphylla*. Nature 182: 540-541.

Cruz, R. D., Branquinho, C., and Silva, J. da. 2008. Oxygen evolution and chlorophyll fluorescence under extreme desiccation in the aquatic bryophyte *Fontinalis antipyretica*. Chapt. 7. In: Allen, J. F., Gantt, E., Golbeck, J. H., and Osmond, B. (eds.). Photosynthesis. Energy from the Sun. Springer, Dordrecht, pp. 1425-1430.

Czeczuga, B. 1971. Carotenoid pigments in the *Bryum ventricosum* Dicks 1785 from the Plevicki Lakes (Yugoslavia). Planta 103: 87-90.

Czeczuga, B. 1980. Investigations on carotenoids in Embryophyta. I. Bryophyta. Bryologist 83: 21-28.

Czeczuga, B. 1985. Investigations on carotenoids in Embryophyta. III. Representatives of the Hepaticae. Phyton 25: 113-121.

Czeczuga, B. 1987. The effect of light on the content of photosynthetically active pigments in plants. VIII. Increase of the content of chlorophylls and carotenoids in aquatic mosses under the influence of green light. Polskie Arch. Hydrobiol. 34: 171-176.

Czeczuga, B., Gutkowski, R., and Czerpak, R. 1982. Investigations of carotenoids in Embryophyta. II. Musci from the Antarctic. Nova Hedw. 36: 695-701.

Davy de Virville, M. A. 1927a. L'action du milieu sur les mousses. Rev. Gen. Bot. 467: 711-726.

Davy de Virville, M. A. 1927b. L'action du milieu sur les mousses. Rev. Gen. Bot. 468: 767-783.

Deltoro, V. I., Calatayud, A., Gimeno, C., and Barreno, E. 1998. Water relations, chlorophyll fluorescence, and membrane permeability during desiccation in bryophytes from xeric, mesic, and hydric environments. Can. J. Bot. 76: 1923-1929.

Dembitsky, V. M. and Rezanka, T. 1995. Distribution of acetylenic acids and polar lipids in some aquatic bryophytes. Phytochemistry 40: 93-97.

Deschamp, P. A. and Cooke, T. J. 1985. Leaf dimorphism in the aquatic angiosperm *Callitriche heterophylla*. Amer. J. Bot. 72: 1377-1387.

Dhindsa, R. S. 1985. Non-autotrophic CO_2 fixation and drought tolerance in mosses. J. Exper. Bot. 36: 980-988.

Dilks, T. J. K. and Proctor, M. C. F. 1975. Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. J. Bryol. 8: 317-336.

Elssmann, E. 1923. Studien über Wasserbewohnende Laubmoose. Hedwigia 64: 52-145.

Evans, G. C., Bainbridge, R., and Rackham, O. 1974. Light as an ecological factor: II. Blackwell Sci. Publ., Oxford.

Everitt, D. T. and Burkholder, J. M. 1991. Seasonal dynamics of microphyte communities from a stream flowing over granite flatrock in North Carolina, U.S.A. Hydrobiologia 222: 159-172.

Ewart, A. J. 1895-1897. On assimilatory inhibition in plants. J. Linn. Soc. Bot. 31: 364-461.

Fabón, G., Martínez-Abaigar, J., Tomás, R., and Núñez-Olivera, E. 2010. Effects of enhanced UV-B radiation on hydroxycinnamic acid derivatives extracted from different cell compartments in the aquatic liverwort *Jungermannia exsertifolia* subsp. *cordifolia*. Physiol. Plant. 140: 269-279.

Fabón, G., Monforte, L., Tomás-Las-Heras, R., Núñez-Olivera, E., and Martínez-Abaigar, J. 2012. Dynamic response of UV-absorbing compounds, quantum yield and the xanthophyll cycle to diel changes in UV-B and photosynthetic radiations in an aquatic liverwort. J. Plant Physiol. 169: 20-26.

Farmer, A. M., Boston, H. L., and Adams, M. S. 1988. Photosynthetic characters of a deepwater bryophyte from a clear, oligotrophic lake in Wisconsin, U.S.A. Verh. Internat. Verein. Limnol. 23: 1912-1915.

Florschütz, P. A., Gradstein S. R., and Rubers, W. V. 1972. The spreading of *Fissidens crassipes* Wils. (Musci) in the Netherlands. Acta Bot. Neerl. 21: 174-179.

Fornwall, M. D. and Glime, J. M. 1982. Cold and warm-adapted phases in *Fontinalis duriaei* Schimp. as evidenced by net assimilatory and respiratory responses to temperature. Aquat. Bot. 13: 165-177.

Glime, J. M. 1971. Response of two species of *Fontinalis* to field isolation from stream water. Bryologist 74: 383-386.

Glime, J. M. 1982. Response of *Fontinalis hypnoides* to seasonal temperature variations. J. Hattori Bot. Lab. 53: 181-193.

Glime, J. M. 1984. Theories on adaptations to high light intensity in the aquatic moss *Fontinalis*. J. Bryol. 13: 257-262.

Glime, J. M. 1996. Aquatic bryoecology. Bryol. Times 87: 2.

Glime, J. M. 2014. Adventures with stream mosses – A *Fontinalis* point of view. Part II: Reproduction. Evansia 31: 114-120.

Glime, J. M. and Acton, D.W. 1979. Temperature effects on assimilation and respiration in the *Fontinalis duriaei*-periphyton association. Bryologist 82: 382-392.

Glime, J. M. and Carr, R. E. 1974. Temperature survival of *Fontinalis novae-angliae* Sull. Bryologist 77: 17-22.

Glime, J. M. and Gradstein, S. R. 2018. Tropics: General Ecology. Chapt. 8-1. In: Glime, J. M. Bryophyte Ecology. Volume 4. Habitat and Role. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 22 July 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology4/>.

Glime, J. M. and Rohwer, F. 1983. The comparative effects of ethylene and 1-amino-cyclopropane-1-carboxylic acid on two species of *Fontinalis*. J. Bryol. 12: 611-616.

Glime, J. M. and Vitt, D. H. 1984. The physiological adaptations of aquatic Musci. Lindbergia 10: 41-52.

Gupta, R. K. 1976. The physiology of the desiccation in bryophytes: Nature of organic compounds leaked from desiccated liverwort *Plagiochila asplenioides*. Biochem. Physiol. Pflanzen 170: 389-395.

Gupta, R. K. 1977a. A note on photosynthesis in relation to water content in liverworts: *Porella platyphylla* and *Scapania undulata*. Austral. J. Bot. 25: 363-365.

Gupta, R. K. 1977b. A study of photosynthesis and leakage of solutes in relation to the desiccation effects in bryophytes. Can. J. Bot. 55: 1186-1194.

Gupta, R. K. 1977c. An artifact in studies of the responses of respiration of bryophytes to desiccation. Can. J. Bot. 55: 1195-1200.

Gupta, R. K. 1978a. Physiology of desiccation resistance in bryophytes: Effect of desiccation on water status and chlorophyll *a* & *b*. Indian J. Exper. Biol. 16: 354-356.

Gupta, R. K. 1978b. Physiology of desiccation resistance in bryophytes: Effect of pre-treatment on desiccation resistance. Indian J. Exper. Biol. 16: 350-353.

Gupta, R. K. 1979. Leakage of photosynthates from water-stressed liverwort *Scapania undulata* (L.) Dum. Indian J. Exper. Biol. 17: 164-166.

Gwozdz, E. A. and Bewley, J. D. 1975. Plant desiccation and protein synthesis: An in vitro system from dry and hydrated mosses using endogenous and synthetic messenger ribonucleic acid. Plant Physiol. 55: 340-345.

Hearnshaw, G. F. and Proctor, M. C. F. 1982. The effect of temperature on the survival of dry bryophytes. New Phytol. 90: 221-228.

Henry, L. K. 1929. The effect of the environment upon mosses. Bryologist 32: 84-87.

Hunek, S. 1983. Chemistry and biochemistry of bryophytes. In: Schuster, R. M. (ed.). New Manual of Bryology. Hattori Botanical Laboratory, Nichinan, pp. 1-116.

Irmscher, E. 1912. Über die Resistenz der Laubmoose gegen Austrocknung und Kälte. Jahr. Wiss. Bot. 50: 387-449.

Johnson, A. and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. Bryologist 73: 683-686.

Karunen, P. 1982. Possible evolutionary significance of galactolipid fatty acids in Bryophyta. J. Hattori Bot. Lab. 53: 255-269.

Kinugawa, K. 1966. The "storage reactivation," photoreactivation and dark recovery from the ultraviolet light induced damage of sporeling of *Bryum pseudotriquetrum*. Misc. Bryol. Lichenol. 4: 56-57.

Kirk, J. T. O. 1994. Light and Photosynthesis in Aquatic Ecosystems. 2nd ed. Cambridge University Press, Cambridge.

Kopacek, J. and Blazka, P. 1994. Ammonium uptake in alpine streams in the High Tatra Mountains (Slovakia). Hydrobiologia 294: 157-165.

Krochko, J. E., Winner, W. E., and Bewley, J. D. 1979. Respiration in relation to adenosine triphosphate content during desiccation and rehydration of a desiccation-tolerant and a desiccation-intolerant moss. Plant Physiol. 64: 13-17.

Kuwabara, A. and Nagata, T. 2006. Cellular basis of developmental plasticity observed in heterophyllous leaf formation of *Ludwigia arcuata* (Onagraceae). Planta 224: 761-770.

Kuwabara, A., Ikegami, K., Koshiba, T., and Nagata, T. 2003. Effects of ethylene and abscisic acid upon heterophylly in *Ludwigia arcuata* (Onagraceae). Planta 217: 880-887.

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. J. N. Amer. Benthol. Soc. 19: 573-592.

Lohammar, G. 1954. The distribution and ecology of *Fissidens julianus* in northern Europe. Svensk Bot. Tidskr. 58: 162-173.

López, J. and Carballeira, A. 1989. A comparative study of pigment contents and response to stress in five species of aquatic bryophytes. Lindbergia 15: 188-194.

Maberly, S. C. 1985. Photosynthesis by *Fontinalis antipyretica*. 1. Interaction between photon irradiance, concentration of carbon dioxide and temperature. New Phytol. 100: 127-140.

Marschall, M. and Proctor, M. C. F. 2004. Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll *a*, chlorophyll *b* and total carotenoids. Ann. Bot. 94: 593-603.

Martin, C. E. and Churchill, S. P. 1982. Chlorophyll concentrations and chlorophyll *a* to chlorophyll *b* ratios in mosses collected from exposed and shaded habitats in Kansas. J. Bryol. 12: 297-304.

Martínez-Abaigar, J. and Núñez-Olivera, E. 1998. Ecophysiology of photosynthetic pigments in aquatic bryophytes. In: Bates, J. W., Ashton, N. W., and Duckett, J. G. (eds.). Bryology for the Twenty-first Century. Maney Publishing and the British Bryological Society, UK, pp. 277-292.

Martínez-Abaigar, J. and Núñez-Olivera, E. 2011. Aquatic bryophytes under ultraviolet radiation. In: Tuba, Z., Slack, N. G., and Stark, L. R. (eds.). Bryophyte Ecology and Climate Change. Cambridge University Press, Cambridge, UK, pp. 115-146.

Martínez-Abaigar, J. and Núñez-Olivera, E. 2018. Ecophysiology of photosynthetic pigments in aquatic bryophytes. Chapt. 18. In: Bates, J. W., Ashton, N. W. and Duckett, J. G. Bryology for the Twenty-first Century.

Martínez-Abaigar, J. and Olivera, E. 2007. Climate change and ultraviolet radiation: Effects on stream bryophytes. Field Bryol. 91: 35-36.

Martínez-Abaigar, J., Núñez-Olivera, E., and Sánchez-Díaz, M. 1994. Seasonal changes in photosynthetic pigment composition of aquatic bryophytes. J. Bryol. 18: 97-113.

Martínez-Abaigar, J., Núñez-Olivera, E., Beaucourt, N., García-Álvaro, M. A., Tomás, R., and Arróniz, M. 2003. Different physiological responses of two aquatic bryophytes to enhanced ultraviolet-B radiation. J. Bryol. 25: 17-30.

Martínez-Abaigar, J., Núñez-Olivera, E., Arróniz-Crespo, M., Tomás, R., Beaucourt, N., and Otero, S. 2004a. Effects of enhanced ultraviolet-B radiation on aquatic bryophytes from mountain streams. Abstract. XV IAB World Congress, p. 44.

Martínez-Abaigar, J., Núñez-Olivera, E., Tomás, R., Beaucourt, N., and García-Álvaro, M. Á., and Arróniz, Y. M 2004b. Daños macroscópicos y microscópicos causados por un aumento de la radiación ultravioleta-B en dos briófitos acuáticos del Parque Natural de Sierra Cebollera (La Rioja, norte de España). [Macroscopic and microscopic damage caused by an increase in ultraviolet-B radiation in two aquatic bryophytes of the Natural Park of Sierra Cebollera (La Rioja, northern Spain).]. Zubía 22: 143-163.

Martínez-Abaigar, J., Núñez-Olivera, E., Arróniz Crespo, M., Tomás, R., Beaucourt, N., and Otero, S. 2006. Effects of ultraviolet radiation on aquatic bryophytes. Limnética 25: 81-94.

Martínez-Abaigar, J., Otero, S., Tomás, R., and Núñez-Olivera, E. 2008. High-level phosphate addition does not modify UV effects in two aquatic bryophytes. Bryologist 111: 444-454.

Martínez-Abaigar, J., Otero, S., Tomás, R., and Núñez-Olivera, E. 2009. Effects of enhanced ultraviolet radiation on six aquatic bryophytes. Cryptog. Bryol. 30: 157-175.

Martins, R. J., Pardo, R., and Boaventura, R. A. 2004. Cadmium (II) and zinc (II) adsorption by the aquatic moss *Fontinalis antipyretica*: Effect of temperature, *p*H and water hardness. Water Res. 38: 693-699.

McCarthy, D. T. 1977. The effects of drainage on the Trimblestown River Ireland I. Benthic invertebrates and flora. Irish Fish. Invest. Ser. A (Freshwat.) 16: 3-16.

Monforte, L., Soriano, G., Núñez-Olivera, E., and Martínez-Abaigar, J. 2018. Cell compartmentation of ultraviolet-absorbing compounds: An underexplored tool related to bryophyte ecology, phylogeny and evolution. Funct. Ecol. 32: 882-893.

Núñez-Olivera, E., Martínez-Abaigar, J., Tomás, R., Beaucourt, N., and Arróniz-Crespo, M. 2004. Influence of temperature on the effects of artificially enhanced UV-B radiation on aquatic bryophytes under laboratory conditions. Photosynthetica 42: 201-212.

Núñez-Olivera, E., Arróniz-Crespo, M., Martínez-Abaigar, J., Tomás, R., and Beaucourt, N. 2005. Assessing the UV-B tolerance of sun and shade samples of two aquatic bryophytes using short-term tests. Bryologist 108: 435-449.

Oechel, W. C. 1976. Seasonal patterns of temperature response of CO_2 flux and acclimation in Arctic mosses growing *in situ*. Photosynthetica 10: 447-456.

Ormerod, S. J., Rundle, S. D., Wilkinson, S. M., Daly, G. P., Dale, K. M., and Juttner, I. 1994. Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. Freshwat. Biol. 32: 309-322.

Otero, S., Nunez-Olivera, E., Martinez-Abaigar, J., Tomás, R., Arróniz-Crespo, M., and Beaucourt, N. 2006. Effects of cadmium and enhanced UV radiation on the physiology and the concentration of UV-absorbing compounds of the aquatic liverwort *Jungermannia exsertifolia* subsp. *cordifolia*. Photochem. Photobiol. Sci. 5: 760-769.

Otero, S., Martinez-Abaigar, K. C. J., and Nunez-Olivera, E. 2008. Ultraviolet-absorbing capacity of aquatic bryophytes from Tierra del Fuego (Argentina). J. Bryol. 30: 290-296.

Otero, S., Núñez-Olivera, E., Martínez-Abaigar, J., Tomás, R., and Huttunen, S. 2009. Retrospective bioindication of stratospheric ozone and ultraviolet radiation using hydroxycinnamic acid derivatives of herbarium samples of an aquatic liverwort. Environ. Pollut. 157: 2335-2344.

Patterson, P. M. 1946. Osmotic values of bryophytes and problems presented by refractory types. Amer. J. Bot. 33: 604-611.

Peñuelas, J. 1984a. Pigments of aquatic mosses of the river Muga, NE Spain, and their response to water pollution. Lindbergia 10: 127-132.

Peñuelas, J. 1984b. Pigment and morphological response to emersion and immersion of some aquatic and terrestrial mosses in N. E. Spain. J. Bryol. 13: 115-128.

Peñuelas, J. and Vallcorba, T. 1988. Spatio-temporal pigment gradient along transverse transects of the Riu Tenes (Catalonia). J. Bryol. 15: 229-232.

Peñuelas, J., Murillo, J., and Azcón-Bieto, J. 1988. Actual and potential dark respiration rates and different electron transport pathways in freshwater aquatic plants. Aquat. Bot. 30: 353-362.

Priddle, J. 1979. Morphology and adaptations of aquatic mosses in an Antarctic lake. J. Bryol. 10: 517-529.

Priddle, J. 1982. Bryophytes in Antarctic lakes. Bull. Brit. Bryol. Soc. 39: 18.

Prins, H. H. Th. 1981. Why are mosses eaten in cold environments only? Oikos 38: 374-380.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. Bot. J. Linn. Soc. 104: 61-77.

Rader, R. B. and Belish, T. A. 1997. Short-term effects of ambient and enhanced UV-B on moss (*Fontinalis neomexicana*) in a mountain stream. J. Freshwat. Ecol. 12: 395-403.

Rice, S. K. 1995. Patterns of allocation and growth in aquatic *Sphagnum* species. Can. J. Bot. 73: 349-359.

Roberts, E. A. and Haring, I. M. 1937. The water relations of the cell walls of certain mosses as a determining factor in their distribution. Ann. Bryol. 10: 97-114.

Saitoh, M., Narita, K., and Isikawa, S. 1970. Photosynthetic nature of some aquatic plants in relation to temperature. Bot. Mag. (Tokyo) 83: 10-12.

Sanford, G. R. 1979. Temperature related growth patterns in *Amblystegium riparium*. Bryologist 82: 525-532.

Sanford, G. R., Bayer, D. E., and Knight, A. W. 1974. An evaluation of environmental factors affecting the distribution of two aquatic mosses in the Sacramento River near Anderson, California. Univ. Calif. Depts. Bot., Water Sci. Eng.

Schmidt-Stohn, G. 1977. Anderungen der Plastidenpigmente bei *Sphagnum magellanicum* Brid. in Abhängigkeit von Standort, Verfärbungsgrad und Alter. Zeit. Pflanzenphysiol. 81: 289-202.

Schröeder, G. 1886. Über die Austrockungsfähigkeit der Pflanzen. Unters. Bot. Inst. Tubingen 2: 1-53.

Soriano, G., Castillo, M. A. del, Monforte, L., Núñez-Olivera, and Martinez-Abaigar, J. 2019. Acclimation of bryophytes to sun conditions, in comparison to shade conditions, is influenced by both photosynthetic and ultraviolet radiations. Front. Plant Sci. 10: 998.

Spitale, D. 2009. Switch between competition and facilitation within a seasonal scale at colony level in bryophytes. Oecologia 160: 471-482.

Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2013. The desert moss *Pterygoneurum lamellatum* (Pottiaceae) exhibits an inducible ecological strategy of desiccation tolerance: Effects of rate of drying on shoot damage and regeneration. Amer. J. Bot. 100: 1522-1531.

Stewart, R. R. C. and Bewley, J. D. 1982. Stability and synthesis of phospholipids during desiccation and rehydration of a desiccation-tolerant and a desiccation-intolerant moss. Plant Physiol. 69: 724-727.

Szarek, E. 1994. The effect of abiotic factors on chlorophyll *a* in attached algae and mosses in the Sucha Woda stream (High Tatra Mts, southern Poland). Acta Hydrobiol. (Cracow) 36: 309-322.

Taylor, J., Thomas, R. J., and Otro, J. G. 1972. Chromatographic and spectrophotometric analysis of the photosynthetic pigments of the gametophyte and the sporophyte of *Lophocolea heterophylla.* Bryologist 75: 36-42.

Thatcher, E. P. 1949. Bryophytes of an artificially illuminated cave. Bryologist 52: 212-214.

Vanderpoorten, A., Klein, J.-P., Stieperaere, H., and Trémolières, M. 1999. Variations of aquatic bryophyte assemblages in the Rhine Rift related to water quality. 1. The Alsatian Rhine floodplain. J. Bryol. 21: 17-23.

Vitt, D. H. and Glime, J. M. 1984. The structural adaptations of aquatic Musci. Lindbergia 10: 95-110.

Vitt, D. H. and Pakarinen, P. 1977. The bryophyte vegetation, production, and organic components of Truelove Lowland. In: Bliss, L. C. (ed.). Truelove Lowland, Devon Island, Canada: A high Arctic Ecosystem. University of Alberta Press, Edmonton, Canada, pp. 225-244.

Vujičić, M., Sabovljević, A., Milošević, S., Segarra-Moragues, J. G., and Sabovljević, M. S. 2016. Effects of abscisic acid (ABA) on the development of selected bryophyte species. Plant Biosyst. 150: 1023-1029.

Wanke, D. 2011. The ABA-mediated switch between submersed and emersed life-styles in aquatic macrophytes. J. Plant Res. 124: 467-475.

Westlake, D. F. and Dawson, F. H. 1976. In: Evans, G. C., Bainbridge, R., and Rackham, O. Light as an ecological factor: II. Blackwell Sci. Publ., Oxford, pp. 27-42.

Wikipedia. 2019. Daylight. Accessed 19 November 2019 at <https://en.wikipedia.org/wiki/Daylight>.

Zastrow, E. 1934. Aquatic moss experiments. Pflanzenforschung 17: 1-70.